THE UNIVERSITY OF ALBERTA

BIOLOGY AND RELATIONSHIPS OF *PTEROSTICHUS ADSTRICTUS* ESCHSCHOLTZ AND *PTEROSTICHUS PENSYLVANICUS* LECONTE (COLEOPTERA : CARABIDAE)

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Biology and Relationships of *Pterostichus adstrictus* Eschscholtz and *Pterostichus pensylvanicus* LeConte (Coleoptera : Carabidae), submitted by Henri Goulet in partial fulfilment of the requirements for the degree of Master of Science.

Date October 13, 1971

Autobiography

I was born in Montreal, Quebec, May 26, 1945. My primary and secondary education were completed at Rigaud, Quebec. Soon, in this beautiful region I became fascinated by nature. My first loves were trees, then mammals. But in the fall of 1961, Father Andre Larochelle interested me in the limitless world of insects. However, during fall not many insects are active, so my interests centred rapidly on ground beetles. I still run after them!

I finished my B.A. at Rigaud in 1966, and went to Macdonald College of McGill University where I obtained a B.Sc. in 1969.

During my undergraduate summers, thanks to G. E. Ball, I had the pleasure of coming to Alberta to study ground beetles. In these summers the present project slowly emerged.

Abstract

Two structurally similar species, *Pterostichus adstrictus* Eschscholtz and *P. pensylvanicus* LeConte, the members of which often live in similar habitats, are compared relative to some of their ecological, behavioural, and morphological characteristics.

Pterostichus adstrictus is a more northern species which ranges from forest litter to open meadow habitats. Females oviposit indiscriminately over a wide soil moisture range. The development of immature stages is rapid in central Alberta. *Pterostichus pensylvanicus*, a more southern species, is restricted to forest litter habitats. Females oviposit mostly in very moist soil. Development of immature stages is slower under conditions in the field, although in the laboratory the rate of development is similar in both species. The differences in structure between these species, in both larval and adult stages, are slight but constant.

More general implications of these facts are discussed. Population fluctuations are probably controlled by weather, moisture level in the soil of oviposition sites, warming capacity of these sites, and by the behaviour of immature stages which results in remaining in these sites. The extent of the northern limit of distribution is probably strongly affected by the warming capacities of the oviposition sites and the behaviour of larvae and pupae in remaining in these sites. The mechanisms preventing the formation of hybrids are precopulatory. Males recognize females of their own species after 'tasting' a chemical substance emitted by the apex of the female abdomen. *P. adstrictus* and *P. pensylvanicus*, though very similar, are not sister species. Their ancestors probably invaded North America at two widely separated geological periods.

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1. Introduction

In the past three decades, numerous works on the biology of carabids have appeared (the main ones: Krogerus, 1948; Lindroth, 1949; Van der Drift, 1951; Thiele, 1964). Most of this work was done in Europe. Lindroth's excellent monograph on Canadian carabids, which solved many taxonomic problems, and which was enriched by most useful ecological and biological notes, opened up ecological research on the carabids of North America. Already a few works have appeared (Rivard, 1964; Johnson, Lawrence, and Ellis, 1966; Carter, 1971; Harris and Whitcomb, 1971; and Kirk, 1971a and 1971b). Unfortunately, the lack of knowledge of immature stages (Ball, 1960), and the difficulty in rearing them makes progress slow.

Very few comparative works on the ecology of related species have appeared. Gilbert (1956) worked on four related species of *Calathus;* Paarman (1966) did field and laboratory studies of two closely related species of *Pterostichus;* and Carter (1971) studied the ecology of four species of *Patrobus*.

Much of the work on related species has been done with primarily an ecologist's outlook. My purpose was to approach a similar type of work with a taxonomist's outlook.

It is amazing that closely related species can live in very similar conditions with no apparent displacement effect. The origin of this apparent co-existence may have had a complex history, and what we see today is probably the result of a very long adjustment period. But two main questions remain: How do very closely related species with very similar requirements co-exist, and what mechanisms are involved in

preventing the formation of hybrids? It is with these two questions in mind that I have approached my work on two closely related species.

Many groups of related species are known to live in similar habitats. But many of these live either in inconstant habitat conditions or in habitats too difficult to investigate. For my studies I chose *P. adstrictus* and *P. pensylvanicus*, as the habitats of both species overlap in the forest litter, and both are common. My attention was focussed on these two species for two other reasons. First, they are especially difficult to separate with certainty, although I found that the specific characters mentioned by Lindroth (1966) are constant. Second, both species have very wide ranges and, because over such a wide area the climate and faunal composition vary, I thought that different evolutionary pressures might exist to which local populations must adapt. These different patterns of adaptation are most interesting as they are clear examples of evolution at work today, and illustrate principles behind speciation. Such results can be realized only through comparative works over the whole range of each species.

2. The Study Area

2.1. Field Station

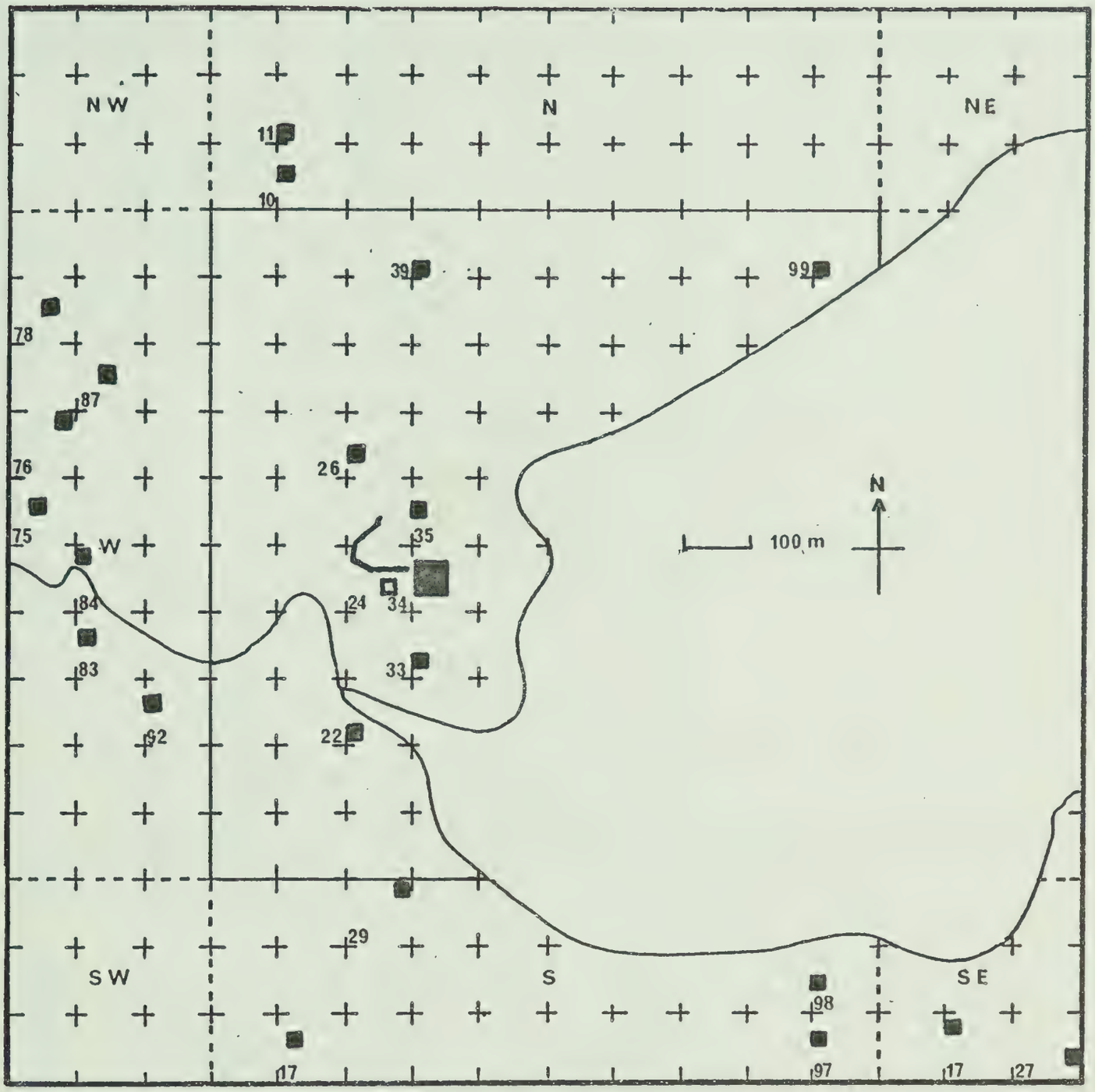
Most of the data were obtained from the George Lake Field Station which is situated about 40 miles northwest of Edmonton, Alberta. The area is north of the parkland zone at the southern edge of the mixed boreal forest (La Roi, 1968). Graham (1969) described the main vegetation types, and Carter (1971) described a grid system permitting rapid location of any particular area at George Lake (Fig. 1).

2.2. Main Habitat Types and the Study Area

To determine the presence, absence, and relative abundance of each species, a wide range of habitats was studied. Data were obtained from forest litter habitats of *Populus tremuloides* Michx., and *P. balsamifera* L., from *Salix* spp., and *Picea glauca* (Moench) stands, and from open land habitats of agricultural lands, *Carex* spp. meadows, *Typha latifolia* L. stands, and dry *Ledum groenlandicum* Oeder bogs. (Details of the collecting sites are included in Section 3.2.2. and Table 1.)

My efforts were concentrated in an area where both species were abundant—in the litter of a deciduous forest comprised of more than 90% *P. tremuloides*. In the underbrush, *Viburnum edule* (Michx.) was uniformly abundant and rose bushes (*Rosa acicularis* Lindl.) were not especially dense.

Fig. 1. Map of George Lake Field Station showing the study area and the distribution of the groups of traps. (The complete numbering system of the grid is indicated on maps available from the Department of Entomology, University of Alberta.)



10 small traps

100 small traps

20 long traps (enclosed)

30 long traps

Table 1. Location of pitfall traps at George Lake, Alberta, in relation to habitat characteristics and grid designation.

Habitat			Grid Designation*
Cover	Dominant Plant	Moisture Conditions	
Forest litter	*Populus tremuloides*	Mesic	26, 24, 34, 97-S, 24
	Populus balsamifera	Mesic to Hygric	11, 10, 33, 39, 29, 99, 17-S, 98-S, 84-W
	Picea glauca	Mesic to Hygric	75-W, 76-W, 17-S
Open	Graminae	Mesic	78-W, 83-W
	Carex rostrata	Hygric	22, 83-W, 27-SE
	Ledum groenlandicum	Xeric	87-W

*For detail see Fig. 1.

3. Materials and Methods

3.1. Materials

The studies described in the following text were based on a total of 5,500 adults and 500 larvae and pupae collected mostly at the George Lake Field Station from 1967 to 1970 (some additional data were obtained from eastern Canada during the period 1961 to 1968). I have also examined adults of *P. oblongopunctatus* Fabricius, *P. mutus* Say, *P. oregonus* Leconte, *P. tropicalis* Bates, *P. ohionis* Csiki, and *P. lustrans* LeConte.

3.2. Field Work

Specimens were obtained by hand collecting, and pitfall trapping. These methods are described below.

3.2.1. Hand Collecting

Specimens were found by searching under stones, logs, and leaves, and in logs, beneath the soil surface, and on plants. The purpose was to determine all of the habitats occupied, as well as the habitat which was apparently most utilized by the immatures and adults of each species. I also observed copulations, and obtained data on other species of carabids associated with *P. adstrictus* and *P. pensylvanicus*. Thus more than 20,000 specimens of carabids were collected.

The most utilized habitat was defined as that habitat which yielded the highest number of specimens per unit area.

Differential effects on capture rate between adults of these two species was very unlikely, but did exist between the immature stages. This method was used to define approximately where *P. pensylvanicus* and *P. adstrictus* adults were more common, and where they were absent.

3.2.2. Pitfall Trapping

In order to determine daily and seasonal locomotory activity, pitfall trapping was used. This method could have led to some information about temporal isolation as an isolating mechanism. Results are expressed in relative units: number of specimens trapped per unit trap per unit time. Pitfall trapping measures only locomotory activity. In carabids, from laboratory evidence, the main activity is expressed through locomotion, and hence the method of pitfall trapping is probably a good relative estimation of activity for adults of the two species. In the text, 'activity' means locomotory movement.

This method is based on the principle that the surface dwellers will walk to a pit and fall into it, and can be prevented from climbing out of it.

The apparatus is very simple. Ordinarily, it consists of a wide-mouthed jar or can which is sunk in the soil up to its rim. Many variations on this theme have been used. A top and/or a funnel, and/or a preserving liquid may be added. The trap may be of different sizes and shapes. In the course of this project I used two main types of pitfall traps. First, I used polyethylene containers (8 cm in diameter and 10 cm deep). I also used two sizes of eavestroughs: the long ones were 1.5 m in length, 10 cm wide, and 7.5 cm deep, and the short ones were 60 cm in length, 7.5 cm wide and 7.5 cm deep. The soil around each trap was tightly packed to reduce the effect of soil shrinkage during dry periods, and the soil was always kept level with the rim. Over each trap a heavy wooden cover was put on three or four pegs about 1.5 cm above the ground for protection of the trap from rain and debris, and the beetles from desiccation and heat from the sun.

In the course of the study, various systems of traps were built (Table 1, Fig. 1). In 1967 I put 20 groups of 10 traps each in various forest litter habitats. In each group, the polyethylene traps were placed about equal distances apart (2.5 m) over 100 square meters. In 1968, I added one more group of 100 polyethylene traps 5 m apart over an area of 2500 square meters. In 1969, I opened a transect made of 30 long eavestroughs, and put 20 short eavestroughs in an enclosed area (2 m apart). Using this method from 1967 to 1970, I trapped 2841 *P. adstrictus* and 2422 *P. pensylvanicus*.

Such a method has numerous weaknesses for estimation of activity. Greenslade (1964) discussed most of them. During my study I discovered a few other points which should be taken into account. (1) Small carabids (less than 7 mm) can climb out on wet walls of the funnel or traps (after a rain or dew deposit). (2) Species running at the bottom of the leaf litter cannot be directly compared with those in it or on the surface of the litter. The difficulty of moving at the bottom of the litter layer is greater than through or over it, as the leaves at the bottom are in smaller pieces and are more compressed. (3) The size of the beetle also affects the results as smaller individuals take more steps per unit length than large ones. (4) The trapping rate is not directly proportional to activity because of mortality and weather effects, and because density per unit area changes in time due to shrinkage or expansion of the area of the suitable habitat. The repellent effect of polyethylene traps was not studied, but it is thought to be weak or absent since the expected number of collected specimens in metal traps, derived from data of polyethylene traps, is very similar to observed data. Scent trails, if any, were not studied.

The adults of the two *Pterostichus* species under study can be compared in various aspects by pitfall trapping, as they move in similar habitats (through leaf litter), and are of approximately the same size. On the other hand, I did not take into account changes in population density due to shrinkage or expansion of the area of the suitable habitat and to mortality. But during the seasonal peak of activity (when the trapping rate was highest), these two variables probably did not play an important role (from May to mid-June). Thus I think that trapping data give a reliable indication of relative activity.

The trapping rate of the larvae was assumed to be proportional to their emergence rate, as the main locomotory activity occurs just after emergence. The trapping rate of tenerals was also assumed to be proportional to their emergence rate. However, the peaks of trapping of tenerals did not correspond directly to emergence peaks because the tenerals remain in the pupal cells for some time.

While collecting from the pitfall traps (every 2 to 3 days throughout the season, and every 2 hours for a study of circadian rhythms), I recorded the number of males and females of each species per trap per unit time, as well as various biological data such as bombarding, copulations, and feeding habits.

3.2.3. Marking and Releasing

As I am interested in differences in relative activity of age groups (the new vs. the old generation adults) and sexes, I marked and released adults of each category. Simultaneously, data were obtained about density and mortality of unmarked adults in the spring.

The marking and releasing method has been used often to estimate population size, even in the study of carabid populations (Greenslade, 1964).

The basic principles are clearly outlined by Southwood (1966).

To prevent migration, an area of 98 square meters was enclosed by a polyethylene fence 30 cm high. The base of the fence was 10 to 15 cm under the soil surface. The upper part of the polyethylene sheet was folded inward to keep adults from climbing out on wet or dirty walls. In the enclosed area, 20 short eavestroughs were distributed in five rows and four columns.

The released specimens were marked with a small cut at the apex of the elytra or by cauterizing a very small area on one interval. Each group of released animals was marked differently (Table 2). These marked adults were obtained from outside the enclosed plot, assuming that little interaction resulted from addition of these to the unmarked population. The mortality rate was probably low in the field during spring and fall, as 70 adults kept in the laboratory did not die during these two periods. Also, in the enclosed area, the mortality rate was probably low, as there were apparently no mice (I found no elytra of eaten adults) and as grouse, probably the main predators, left no trace of digging spots during the period of study.

The collected data yielded information about density and relative activity of each sex. These data were calculated the following way:

To estimate the percentage of unmarked or marked trapped females, the following equation was used:

$$\% \text{ of trapped females} = \left(\frac{B}{A + B}\right) \times 100$$

where: A is the number of trapped males, and

B is the number of trapped females.

If the marked released adults have the same proportion of old and new

Table 2. Number of marked and captured males and females, the percentage of captured and marked females, and the relative activity of each sex for *P. adstrictus* and *P. pensylvanicus*.

Species	Collecting Period	Category of adults	Number released		Number captured		Ratio of captured to released adults	Percentage of released females	Percentage of captured females	*Relative female activity
			M	F	M	F				M vs. F
P. adstrictus	Fall	Old marked	18	33	4	7	0.22	35	64	M < F
		New marked	50	50	5	7	0.12	50	63	M = F
		Unmarked	0	0	1	4	----	--	80	---------
	Spring	Old marked	18	33	6	20	----	35	77	M < F
		New marked	50	50	2	11	----	50	85	M < F
		Mixed marked	25	25	11	10	0.42	50	48	M = F
		Unmarked	0	0	15	5	----	--	25	---------
P. pensylvanicus	Fall	Old marked	10	19	11	7	0.62	66	39	M > F
		New marked	31	23	15	11	0.48	43	42	M = F
		Unmarked	0	0	21	14	----	--	40	---------
	Spring	Old marked	10	19	0	19	----	66	100	M < F
		New marked	31	23	0	7	----	43	100	M < F
		Mixed marked	25	25	8	11	0.38	50	58	M = F
		Unmarked	0	0	5	19	----	--	80	---------

*Was roughly estimated by comparing the percentage of released to captured females.

adults as the unmarked population, then the density of the unmarked population per square meter is calculated as follows:

$$\text{number of unmarked adults per square meter} = \frac{BC}{AG}$$

where: A is the number of trapped marked adults,

B is the number of released marked adults,

C is the number of captured unmarked adults, and

G is the enclosed area in square meters.

3.3. Laboratory Work

3.3.1. Dissection of Females

Data have been published (Rivard, 1964) giving the number of females with mature eggs, and the average content per female. This method shows the period during which females are gravid, but more data are available on the minimal age of the female, and the average number of eggs per female during the reproductive period which permits better understanding of the pattern of oviposition.

In 1968, 127 females of *P. adstrictus* and 43 females of *P. pensylvanicus* were collected and stored in 70% alcohol with the date of collection for later examination. In 1970, 28 females of *P. adstrictus* and 35 females of *P. pensylvanicus* were collected and dissected immediately. The dissections were made under a Wild binocular microscope at 25X magnification. For each female, I recorded the date of collection, presence of larger parasites, the development of the *corpora lutea* (for freshly killed specimens only), and the number of eggs at least 0.75 times as big as the mature eggs.

3.3.2. Morphology

Because adults of these two species were very difficult to separate, other morphological characteristics were sought which would permit decisive

separation. I studied internal organs of males and females as well as their external morphology. To determine the relationships of these two species, five other related species were similarly analysed. I also looked for characteristics differentiating the species at the larval stage.

The morphological studies were based on the examination of 127 females, 10 males, 20 first instar larvae, 20 second instar larvae, and 20 third instar larvae of *P. adstrictus*, and 43 females, 10 males, 20 first instar larvae, 20 second instar larvae, and 20 third instar larvae of *P. pensylvanicus*. I studied the internal and external morphology of both sexes of *P. mutus*, *P. lustrans*, *P. ohionis*, *P. tropicalis*, *P. oregonus*, and *P. oblongopunctatus*. Dry adults were dissected according to Becker's method (Becker, 1958). I followed Schuler's nomenclature of female genitalia (Schuler, 1965).

Measurements were made with an ocular micrometer in a Wild binocular microscope. The elytral length (from the apex of the scutum to the apex of the elytra), and the pronotal length (along the midline between the apex and base of the pronotum) were measured at 10X magnification. Twenty-five specimens of each sex of each species were measured.

3.3.3. Volatile Sex Attractants

Many behavioural reactions between individuals, especially in insects, are governed by pheromones. These chemical substances may repel or attract, may be permanent or temporary, and may be recognized at a distance (if volatile) or on contact. The pheromones of interest here are those permitting species, sex, or species and sex recognition, as they may play an important role as isolating mechanisms. From laboratory data there is little doubt that these chemical messages, if present, are temporary, as females were receptive only for short periods of time. The object of the experiment

was to test if females emit volatile pheromones to attract males.

If females emit some volatile chemical to attract males of their own species, then males released in a choice chamber should be attracted to females of their own species. The use of virgin females in this test is preferable because it is possible that in the species being tested, mating occurs only once.

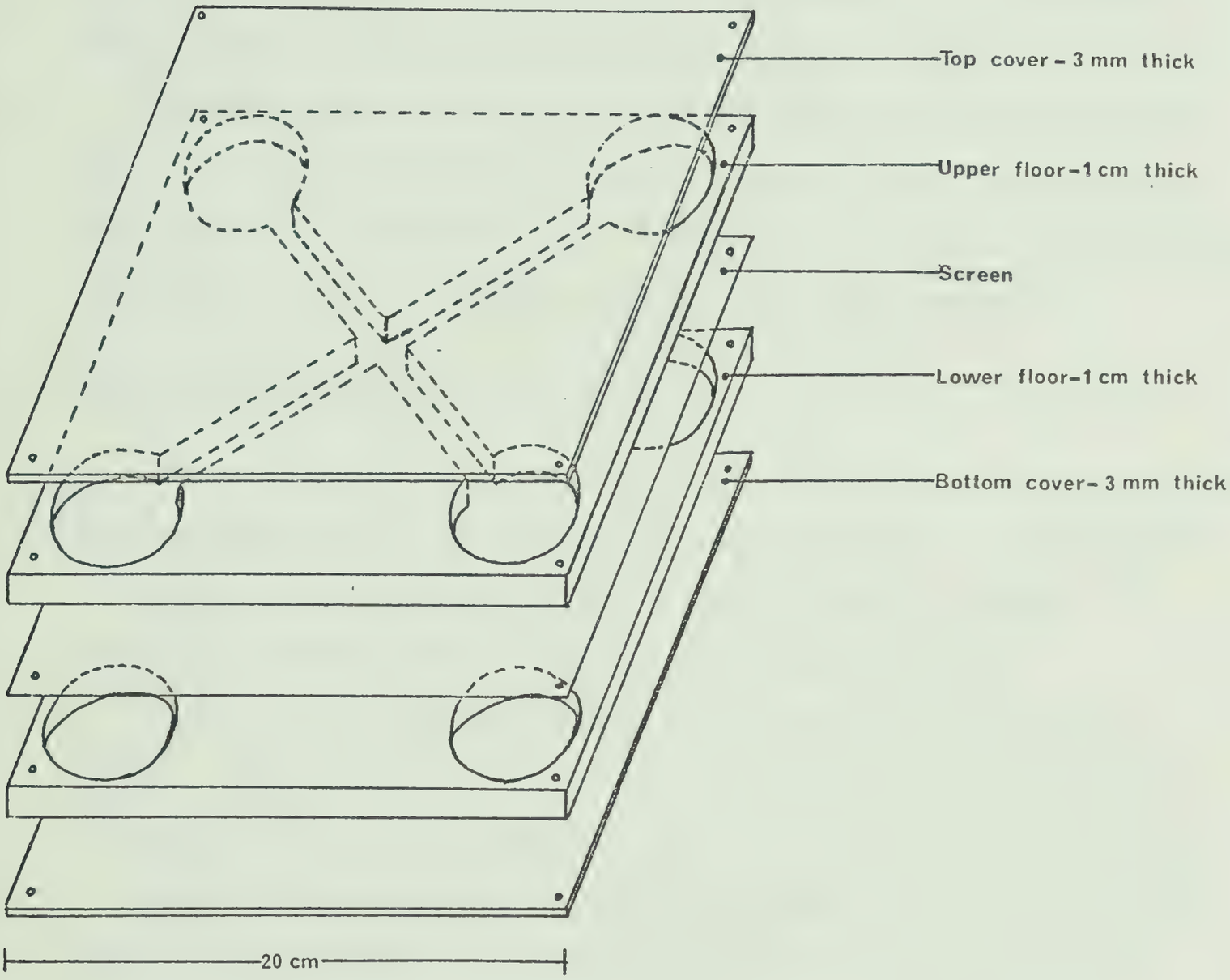
To investigate if males were attracted to virgin females, I built an apparatus (20 cm by 20 cm) consisting of two plexiglass floors separated by a nylon screen. Each floor had four holes which fit exactly over each other except that those of the upper floor were interconnected (Fig. 2). In each of the holes of the lower floor I put five specimens of one sex of one species (each hole had a different sex and species). On the upper floor I liberated 10 males of the species to be studied. I put a moist paper in each of the holes in the lower floor to insure saturation of the atmosphere. I took data on the position of the males on the upper floor relative to what was on the lower floor every hour for 24 hours. The experiments were done at 20 C in an incubator within normal daylight hours under diffused artificial light conditions from the incubator ceiling.

3.3.4. Mating Experiments

The recognition of females of the same species is an important isolating mechanism. If mating is relatively easy to observe, then behavioural study in the laboratory may shed some light on the principles of female recognition.

How do males of each species recognize females of their own species? The ability of the males to distinguish females was investigated by offering the males similar and different species of females, and by direct observation

Fig. 2. Apparatus used to test for the presence or absence of volatile female sex attractants.


Top cover - 3 mm thick
Upper floor - 1 cm thick
Screen
Lower floor - 1 cm thick
Bottom cover - 3 mm thick
20 cm

of the approach of the male to the female.

I put 50 males of each species with females of the same species, then 25 males with females of the other species, and 25 males with females of both species. Each pair or trio was placed in a small plastic vial (35 mm in diameter by 70 mm in height). In each vial I placed wet paper and food. Every two or four hours I checked for mating pairs.

The direct observation of copulation was made by placing two to four males and five to six well-fed females in a plastic box (15 cm by 7.5 cm by 4 cm) with 1.0 cm of moist peat moss. I observed how the males approached the females and the reaction of a mating pair to being separated.

3.3.5. Preferendum Experiments.

3.3.5.1. *Soil Moisture.* Eggs are most sensitive to soil dryness. Thus, the female behaviour in relation to soil moisture may play an important role in the survival of the eggs, especially during periods of drought. To investigate this behaviour, the following experiment was made.

Soils of various moisture content were offered to females of each species. Each soil sample was replicated five times. The preference was determined by the average number of eggs per concentrate of soil moisture.

I used a plexiglass cage (interior measurements: 37 cm by 37 cm by 1 cm high). The floor of the cage consisted of 25 holes (55 mm in diameter) distributed over a grid (5 by 5). The cover consisted of a 3 mm sheet of plexiglass with a small hole (which was closed during experiments) through which females were introduced. Each hole supported a small dish (1 cm by 54 mm diameter) with peat moss. Each dish had its own concentration of soil moisture. Each moisture concentration, replicated five times, was made of 90 ml of air dried peat moss, and the following quantities of water:

A, 0 ml; B, 20 ml; C, 40 ml; D, 60 ml; and E, 80 ml. Finally, these small dishes were distributed in Latin Square fashion (modified from Doane, 1967).

I used 25 well-fed females of one of the species in each experiment. I kept the females for five to six days in the apparatus at 20 C. During this period the beetles were fed once more with pieces of fresh *Tenebrio* larvae. At the end of the experiment, the eggs were counted and the number recorded with the data for each moisture concentration.

As all the sides of the apparatus were surrounded by transparent cello-tape, very little moisture was lost (the plexiglass apparently reacted to differences in relative humidity between the outer and inner surfaces). I did not notice any significant changes in soil moisture as the weight of each dish did not change from the beginning to the end of the experiment. As the beetles could dig easily in the soil, there were no marked differences in the results among the center, edge, and corner data due to thigmotaxis.

3.3.5.2. *Soil Compression.* I think that the difficulty in penetrating logs due to compression of the frass is an explanation of why *P. adstrictus* females oviposit in logs and *P. pensylvanicus* females oviposit in the soil below the litter. The experiment was set up as in the preceding experiment except that I used five different densities, expressed as kilograms per unit area, at moisture 'D' as follows: A, 0 kg; B, 0.5 kg; C, 1.0 kg; D, 1.5 kg; and E, 2.0 kg.

In the previous experiments I noticed that a pressure per unit area of 2.0 kg was the maximum pressure for maximum compression of moist peat moss (without its bouncing back after application of the pressure). Before I applied the pressure to the peat moss, I made sure that the moss in each dish was loose. For the application of the pressure, I used a slightly smaller

dish placed above the peat moss (already in the larger dish); above the smaller dish I put a container with the prescribed weight.

3.3.5.3. *Soil Structure.* In this experiment I wanted to test if females would oviposit on materials normally subject to very rapid drying (such as flat piece of paper, similar in some respects to leaves in the litter), or if they would oviposit in materials which are not normally subject to rapid drying (granular materials, such as sand, peat moss).

Females of each species were offered a moist substrate on which to oviposit. As all the females used in the experiment were in their oviposition period, major differences in oviposition rate observed on the various substrates were probably due to the nature of the substrate used.

Two main substrates were studied: a granular substrate, and a non-granular one. The granular substrate consisted of sifted forest soil, peat moss, and sand; the non-granular one consisted of absorbent paper. I placed the already moistened substrate to be studied in a plastic box (7.5 cm by 15 cm by 3 cm) with ten females (kept well fed). Each day the eggs were counted in each treatment for six days. These experiments were carried out under laboratory conditions.

3.3.6. Oviposition

Because I emphasize the importance of the female behaviour and the egg characteristics, methods used to induce oviposition are here described.

Females were collected in the field by pitfall trapping. They were kept under various conditions of moisture, temperature, substrates and density (Table 3).

Table 3. Number of females kept for specified experiments under the described conditions of temperature, substrate, and period of captivity for *P. adstrictus* (a) and *P. pensylvanicus* (p).

Conditions		Oviposition Experiments							
		Kept in a group of 10		Kept singly		Kept for soil moisture preference as a group of 25		Kept for soil density preference as a group of 25	
		a	p	a	p	a	p	a	p
Temperature	Laboratory	50	50	2	6	0	0	0	0
	Incubator (20C.)	30	30	0	0	25	25	25	25
	Cooler	40	40	11	10	0	0	0	0
Substrate	Sifted forest soil	30	30	13	16	0	0	0	0
	Sifted peat moss	70	70	0	0	25	25	25	25
	Sifted sand	10	10	0	0	0	0	0	0
	Absorbing paper	10	10	0	0	0	0	0	0
Time kept	48 hours	40	40	2	6	25	25	25	25
	less than 48 hours	80	80	11	10	0	0	0	0

For oviposition rate per day over the season, I used groups of 10 females in plastic boxes (15 cm by 7.5 cm by 3 cm) with a moist substrate, under the conditions shown in Table 3. I also placed single females in small boxes (5 cm by 5 cm). I fed each female every other day with one-fifth of a *Tenebrio* larva. The eggs were collected and counted every day, or every four hours (for daily oviposition study), and the soil in which they were laying was replaced with fresh soil after the eggs were counted.

The count of eggs by searching was not exact as some eggs usually escaped observation (0% to 10%). For a precise count (when it was necessary) I floated the eggs by a method described in Southwood (1966), using a saturated sugar solution.

3.3.6.1. *Eggs*. The effects of moisture and temperature on the survival proportion and developmental rate of eggs may be important in function of population changes from year to year. They were tested as follows.

Some of the eggs were incubated in a small box (5 cm by 5 cm) in which there was a small table. On this table was a piece of moist paper on which the eggs were deposited. On the bottom of the box was a 2 mm thick layer of very dilute detergent solution (two to four drops of detergent per 100 ml of water). On emergence the young larvae move about on the table and soon fall and sink in the solution where they become inactive. If the temperature around the incubating box is less than 20 C, the larvae survive in the solution for more than 12 hours.

Some experiments were conducted at field temperatures, others at laboratory and incubator temperatures (Table 4). For precise data, eggs were collected 24 hours after the females were introduced (damaged eggs were discarded). During incubation, eggs covered by fungi were removed to avoid

Table 4. Number of eggs used in experiments to determine water absorption and incubation period of eggs under the specified temperature conditions for *P. adstrictus* (a) and *P. pensylvanicus* (p).

Conditions of temperature	Absorption of water by the eggs		Incubation period	
	a	p	a	p
Laboratory	0	0	3300+	1200+
Incubator (20 C.)	8	8	83	19
Cooler	0	0	20	15

contamination of other eggs. The original number of eggs collected and the number which hatched were recorded.

3.3.6.2. *Larvae and Pupae.* Because of the importance of larval and pupal development rates in the success of adult emergence before winter, the effect of temperature on the development rate was studied as follows.

I reared 10 larvae of each species in the incubator until emergence under conditions of constant temperature (20 C) with day length similar to that in natural conditions. The larvae were reared individually in small plastic containers (20 mm by 35 mm diameter) on a substrate of moist peat moss. The larvae were fed, the old food was removed, and if the moss had too many fungi, I replaced it every two days; this method is slightly modified from Thiele (1968a).

4. Distribution, Ecology, and Morphology

4.1. *Pterostichus pensylvanicus*

4.1.1. Geographical Distribution

The range of this strictly American species is from the southern edge of the boreal forest as far south as at least Pennsylvania, in central North America north of the prairies, and in the west in southern British Columbia, and from Newfoundland in the east to central British Columbia in the west (Lindroth, 1966).

4.1.2. Habitat

Specimens of this species may be obtained only in the forest litter (Lindroth, 1955, 1966). The adults are commonly collected under leaf litter, but not under bark or in rotten logs. In the center of its distribution (southern Quebec), specimens of this species occur in most forest litter habitats (litter of deciduous and coniferous forests under moist conditions and in open or dark conditions). In central Alberta, they are restricted to the litter of deciduous forests on moist soil in more or less exposed conditions only.

The immature stages were collected in the general conditions described above. The eggs are probably laid in the soil in moist areas (none were collected in the field). The larvae occur below the leaves as well as in the soil. The pupae are probably in the soil as they were absent from the logs (none were collected in the field).

4.1.3. Ecological Characteristics

4.1.3.1. *Cycle*. In the spring, overwintering adults become active. These adults may be young ones which emerged the previous fall, or may be

more than a year old. These adults then search for food and mates. This period of high activity continues from the end of April or early May to the end of May or early June. Then the adults become less and less active until the end of June when they enter a summer quiescent period. During the spring period the females oviposit usually from mid-May to the last week of June when they become spent before entering the quiescent period.

The young embryos develop and hatch from mid-June until the last week of July. The larval stage is completed by September. At the end of the third instar, each larva builds a pupating cell (about 2 cm by 1 cm) and becomes quiescent until pupation. A few days before pupation the larvae remain on their backs, insuring a similar position for the pupae. The pupal stage generally takes place from early August until late September. Finally new adults emerge, but they remain in the pupal cells for a few days until the cuticle hardens and becomes dark. Then both the young and old adults become active again in the forest litter. The young adults often mate at this time, although the females do not oviposit. This renewed activity goes on until the soil freezes, usually at the end of October or in early November in central Alberta. As the soil freezes the adults dig under rocks or in the soil or in logs. Often the diapausing adults form aggregates of 20 or more, although solitary specimens were observed frequently in southern Quebec.

4.1.3.2. *Adults.*

(a) *Relative activity of each sex and age-group.* The data on the marking-releasing, and capture-recapture, are in Table 2 (calculations of these data are in Section 3.2.3.).

During the fall, the old generation of marked adults was slightly more active than the new generation of adults. The old generation in the unmarked

population represented 33% of captures. In the old generation adults, the females were apparently less active than the males; but in the new generation adults, the females were probably about as active as the males.

In the spring of 1970, as the released marked mixed adults suggested, the males were probably as active as the females, thus the capture of 80% of unmarked females suggests a high male mortality. The density during this period was estimated at 0.61 specimens per square meter.

(b) *Activity cycle as inferred from the capture rate.*

Seasonal Cycle

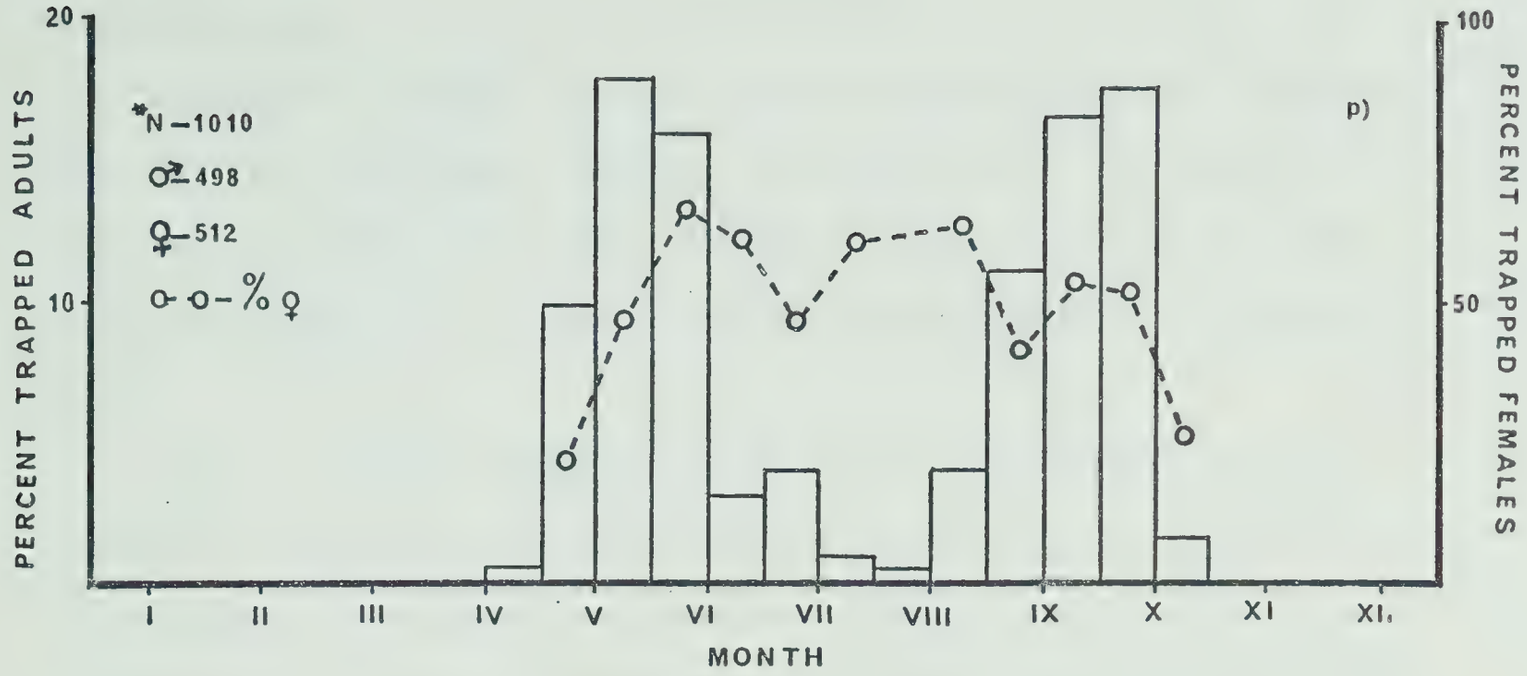
The activity cycle was similar from year to year (as illustrated for 1969 in Fig. 3). In early spring there was an outburst of activity which increased or remained high until the end of May or early June. Then the rate decreased very quickly until late June when very few specimens were trapped. This second period was probably a period of quiescence which lasted at least until mid-August. Another increase in activity followed, reaching its peak between the end of September and mid-October. This peak showed a small increase in activity in the old generation but most of it was due to the newly emerged adults. This peak may decrease by itself or be interrupted abruptly by the beginning of winter (as observed in 1969 and 1970).

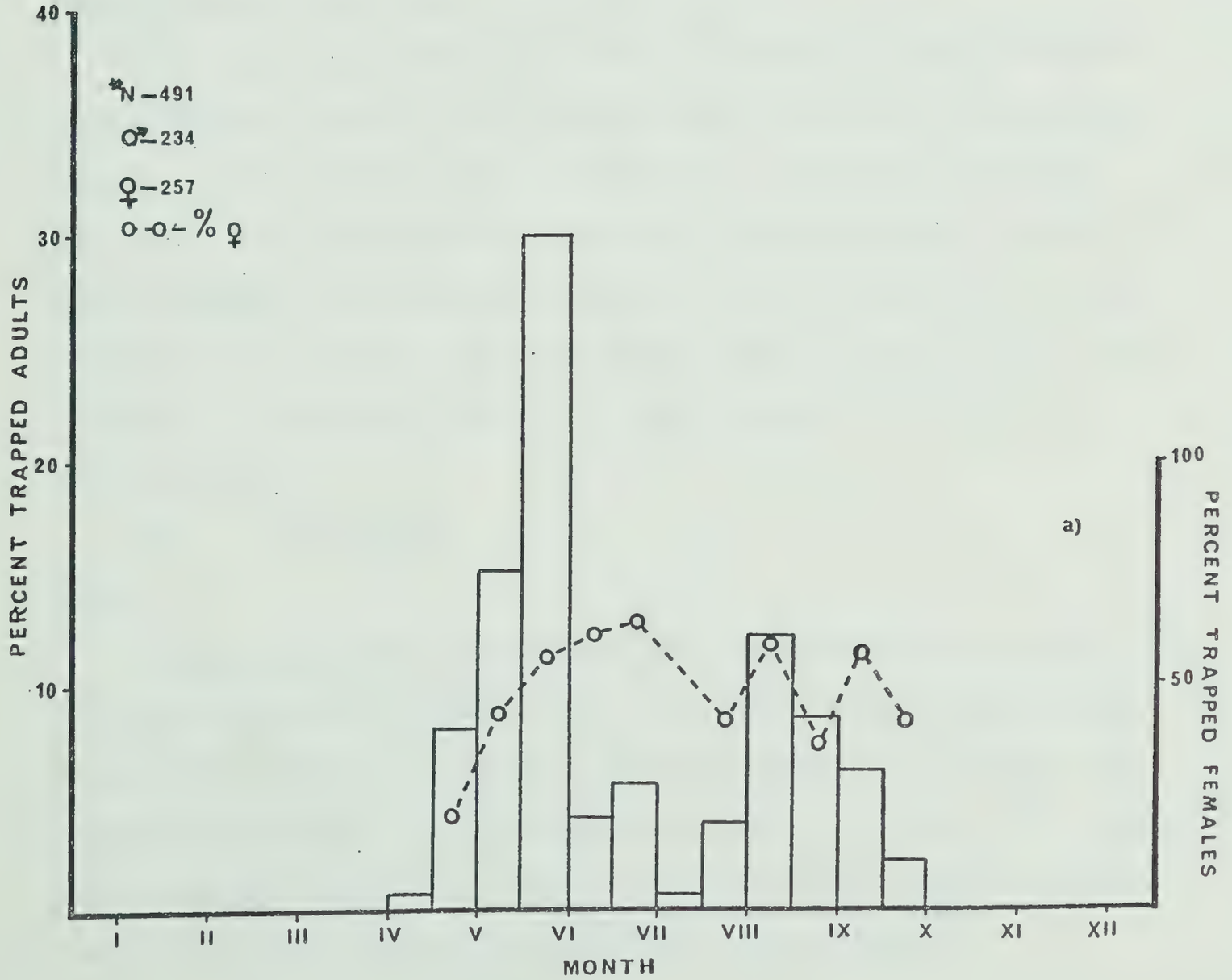
The trapping rate showed differences in activity between the sexes (Fig. 3). The males showed a higher trapping rate in very early spring following which there was an increase in the female trapping rate. The female trapping rate peaked just after the trapping rate for the whole population began to decrease. In the early fall when adults were emerging, the females were trapped at a rate similar to the males.

Fig. 3. Frequency distribution, in 15-day intervals, of captured adults and their sex ratio in 1969.

a) *P. adstrictus*

p) *P. pensylvanicus*





*N = total number of trapped adults

Circadian Cycle

The highest trapping rate was reached around midnight (as an example see Fig. 4). This clearly suggests a nocturnal habit. The increase and decrease of activity was gradual. However, in late fall when the night temperature was below 0 C, most specimens were collected in the daylight hours.

(c) *Mating*. Mating occurred in late fall (Chymko, personal communication) during emergence of new adults, and in early spring until early June (16 copulations were observed in pitfall traps). Couples were observed both at night and during the day. Mating lasted about 12 hours under laboratory conditions.

In the laboratory, males mated only with females of their own species even if offered females of both species, and did not mate if offered only females of the related species, *P. adstrictus*. I observed 15 matings in 75 trials. Thus, there must be a mechanism involved in female recognition. With the apparatus described in Section 3.3.3., I investigated if volatile pheromones were involved. The data shown in Table 5 clearly indicate that males are not especially attracted to virgin females in the absence of physical contact.

(d) *Oviposition*.

Cycle

Oviposition extended from mid-May until the last week of June (Fig. 5). In 1970, the maximum oviposition rate was reached on May 10 from specimens freshly collected but kept at 20 C. Dissected females also showed a low average number of eggs per female before mid-May in 1967 (Fig. 6). In 1969, 99% of the eggs were laid by June 21, and after mid-June eggs were rarely collected (in 1968 and 1970 similar results were obtained).

Fig. 4. Distribution of adults captured at two-hour intervals at George Lake in early June, 1969.

a) *P. adstrictus*

p) *P. pensylvanicus*

Fig. 5. Frequency distribution of eggs laid per five-day interval in 1969 under temperature conditions approximating field conditions and natural light and day length conditions.

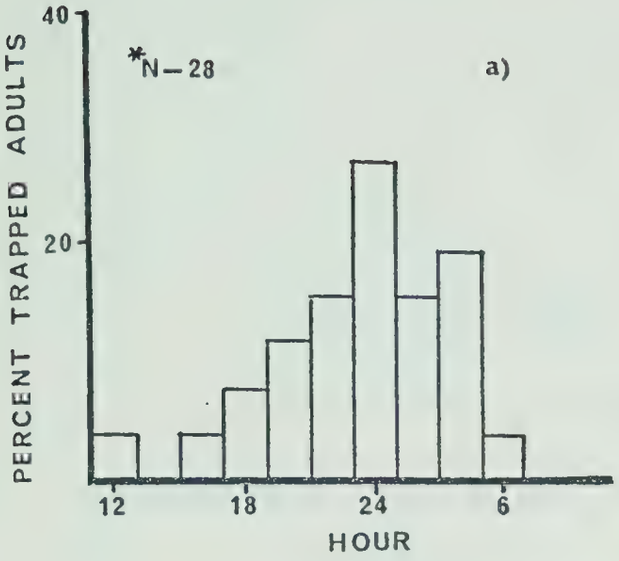
a) *P. adstrictus*

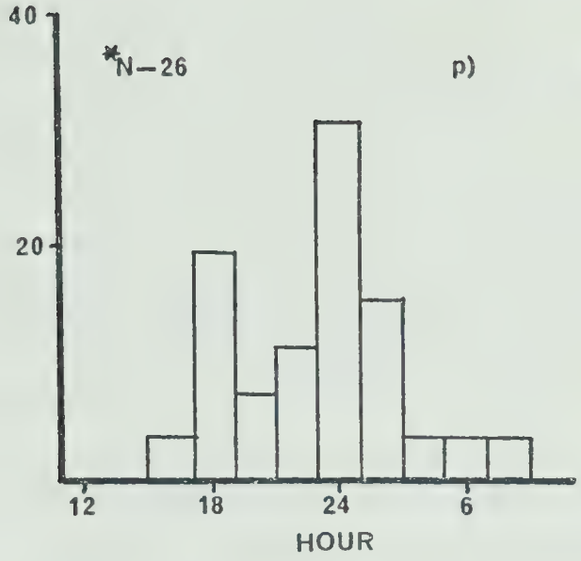
p) *P. pensylvanicus*

Fig. 6. Frequency distribution of average number of eggs per dissected female per five-day interval.

a) *P. adstrictus*

p) *P. pensylvanicus*





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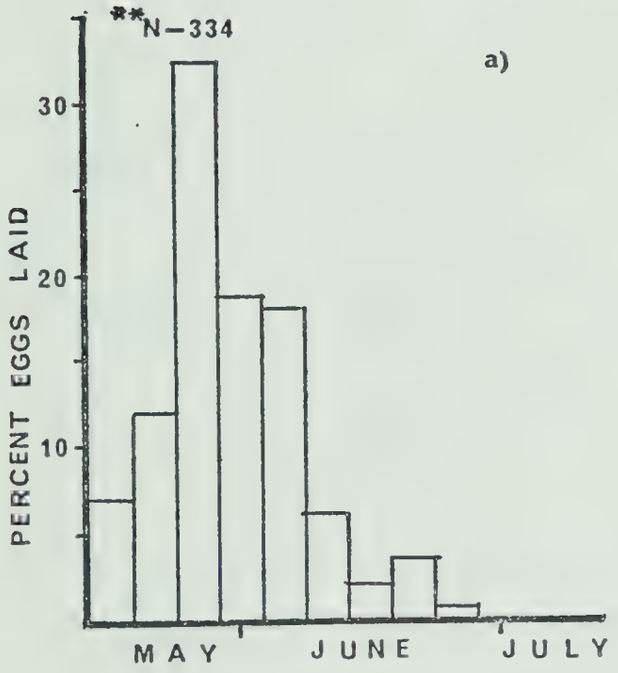

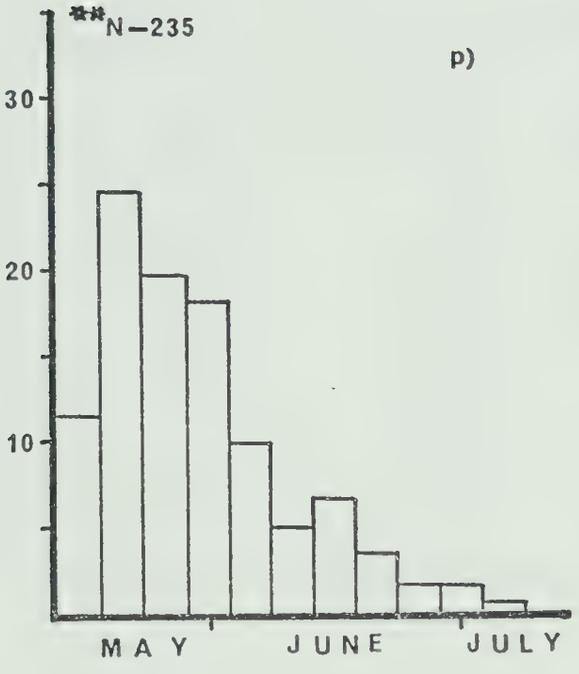

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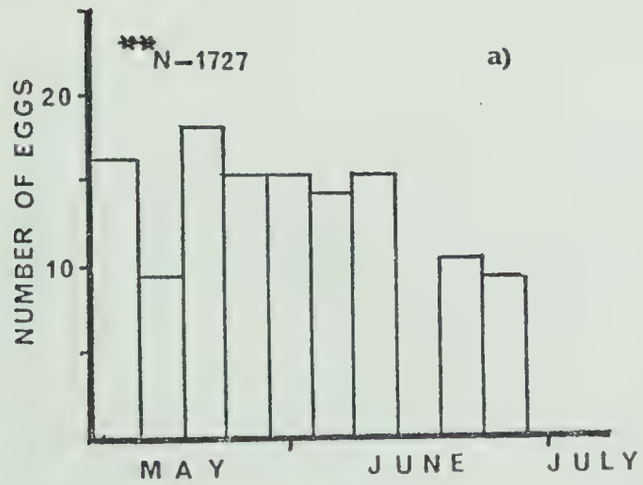
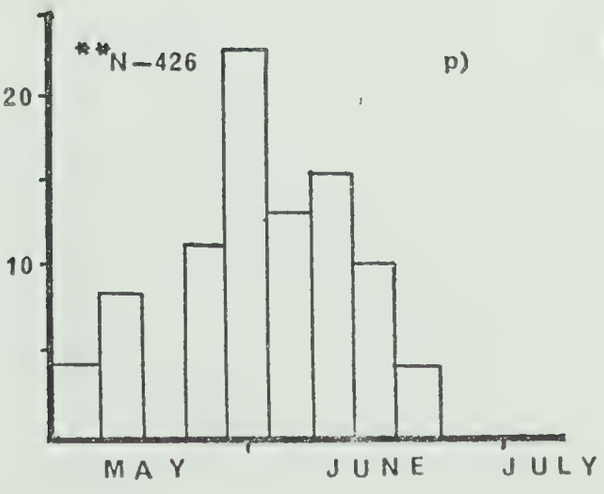




6

*N = total number of trapped adults
**N = total number of eggs

Table 5. Average occurrence in 25 readings of 10 males of the tested species per chamber of the test apparatus on the upper floor, in relation to the sex and species on the lower floor.

Sex	Species on the lower floor	Average number of males on the upper floor per chamber			
		Species			
		P. adstrictus		*P. pensylvanicus*	
		$\bar{x}$	± CL*	$\bar{x}$	± CL
Males	*P. adstrictus*	1.92	0.54	1.28	0.54
	P. pensylvanicus	1.96	0.67	1.40	0.10
Females	*P. adstrictus*	1.72	0.50	1.44	0.63
	P. pensylvanicus	1.88	0.74	1.16	0.64
	---------	3.52	----	4.72	----

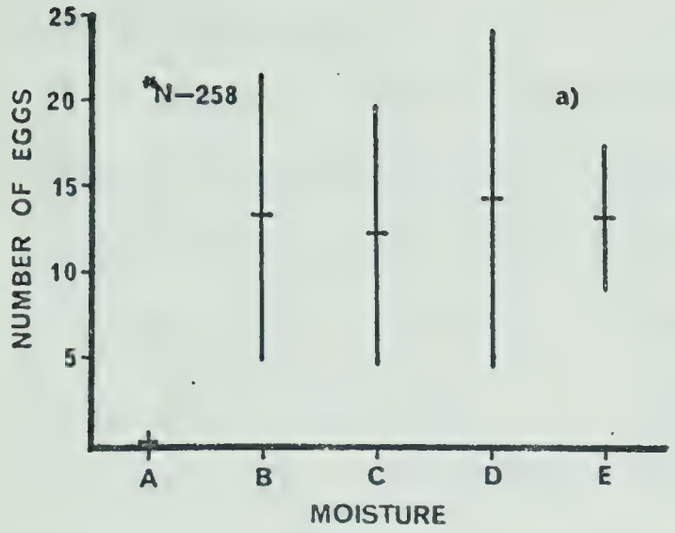
*CL means 95% confidence limit

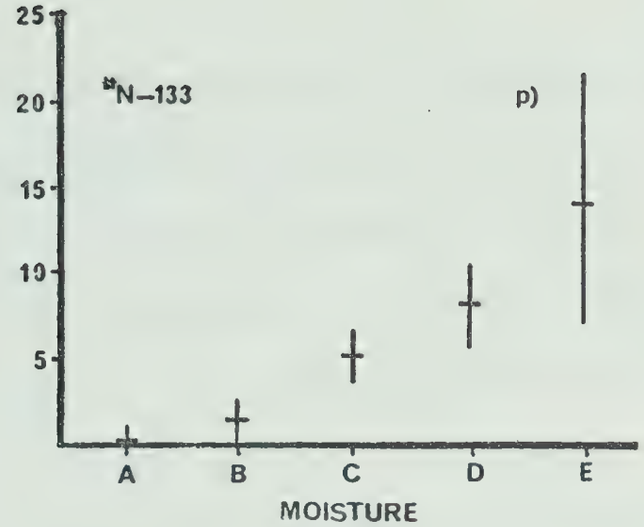
Fig. 7. Average number of eggs laid by 25 females for six days in a cup of a given soil moisture.
The mean is represented by a horizontal line.
95% confidence limit is represented by a vertical line.
a) *P. adstrictus*
p) *P. pensylvanicus*

Fig. 8. Average number of eggs laid by 25 females in a cup of a given soil density in six days.
The mean is represented by a horizontal line.
95% confidence limit is represented by a vertical line.
a) *P. adstrictus*
p) *P. pensylvanicus*

Fig. 9. Number of adults of *P. adstrictus* and *P. pensylvanicus* collected per 200 pitfall traps during June at George Lake for the period 1967 to 1970.
——— *P. adstrictus*
- - - *P. pensylvanicus*

Fig. 10. Diagram illustrating hypothesized changes in relative abundance of adults of *P. pensylvanicus* and *P. adstrictus* at George Lake for the period 1967 to 1970.
——— *P. adstrictus*
- - - *P. pensylvanicus*





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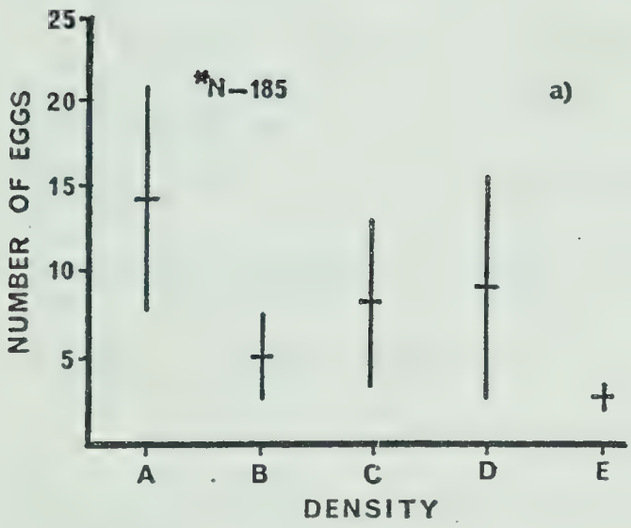

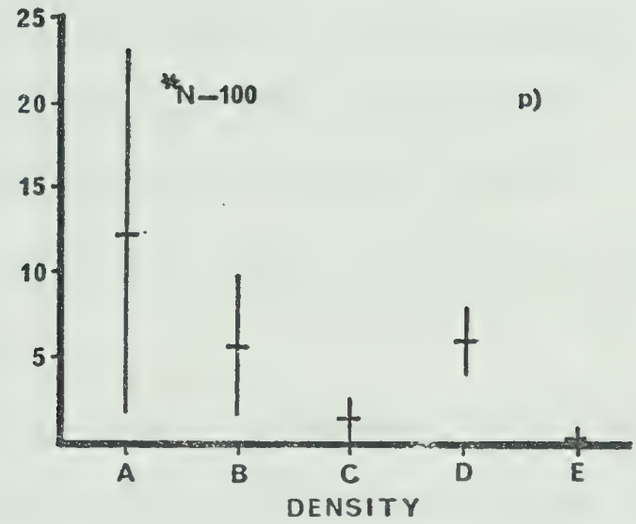

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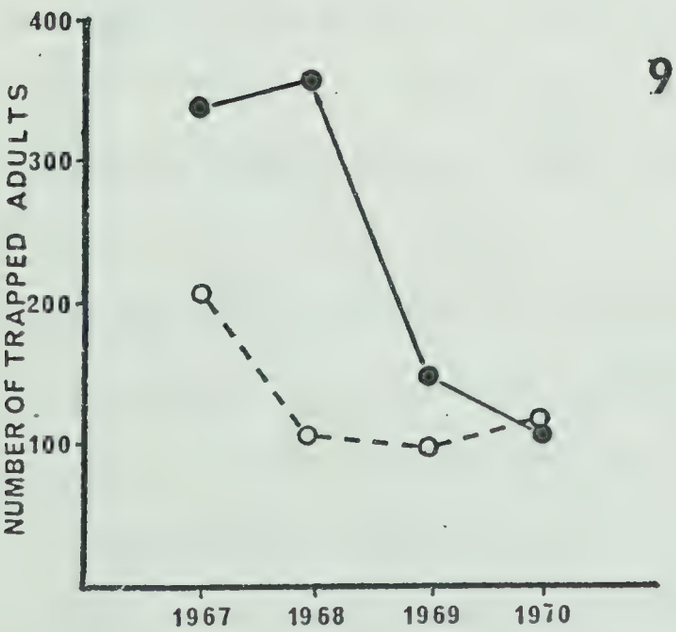

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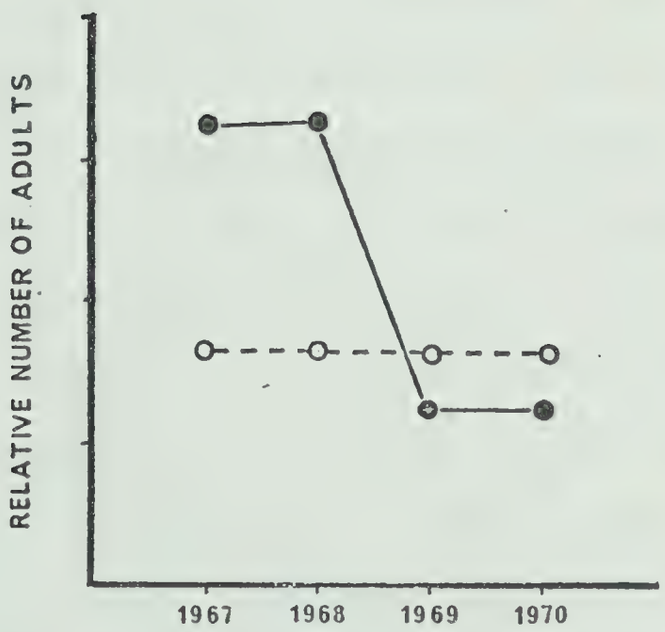


10

*N = total number of eggs

Analysis of Ovaries

The average number of eggs per dissected female over the oviposition season (May and June) was 9.9. This average number obviously does not represent the egg production of each female over the reproductive period, as females laid an average of 22 eggs under temperature conditions approximating field conditions. The average number of eggs varied throughout the season (Fig. 6). In very early spring, there were no eggs. During May the average increased. After mid-June the average number of eggs per female decreased rapidly and by the end of June most females were spent.

In early spring, 11 of 23 dissected females had very well-developed *corpora lutea*. So about half the population may be new adults from the previous fall, and the other half may be more than a year old, as those with well-developed *corpora lutea* have laid eggs during the previous summer.

Pattern of Egg Production

When females were brought into the laboratory, they laid a large number of eggs within two or three days; then, they laid only a few eggs (Table 6). The average number for another ten females kept singly in conditions approximating field conditions was 9.0 eggs over three days (extrapolated from data in Table 7). This average is close to the average number of eggs (9.9 eggs per female) found in dissected females. The average production per female was 0.6 eggs daily for the oviposition season. This does not explain the average production of 9.0 eggs in three days mentioned above. As the average peak production corresponded closely to the average number of mature eggs per female, it is postulated that eggs are laid in batches after being accumulated for some time, and a batch is thought to be as large as the total mature egg content of the female abdomen. Assuming that no eggs are laid between batches, it probably takes two weeks for another batch to develop.

Table 6. Number of eggs per day laid by single females of *P. adstrictus* and *P. pensylvanicus* over a period of 10 days.

Species	Specimen designation	Mean egg production per day	Day Number									
			1	2	3	4	5	6	7	8	9	10
			Number of eggs per day									
P. adstrictus	1	4.0	22	1	7	3	5	2	4	2	5	1
	2	4.6	0	23	0	0	8	0	9	4	1	5
P. pensylvanicus	1	3.1	1	7	8	2	1	5	2	5	0	0
	2	0.6	0	0	3	2	1	0	0	0	0	0
	3	0.8	1	2	3	1	0	1	0	0	0	0
	4	1.0	2	5	1	0	1	1	0	0	0	0
	5	0.3	1	0	1	1	0	0	0	0	0	0

Table 7. Number of eggs laid by each of 10 females of *P. adstrictus* and *P. pensylvanicus* in 24 hours over two days under temperature regimen approximating field conditions.

Species	Day	Specimen Designation									
		1	2	3	4	5	6	7	8	9	10
		Number of Eggs per Specimen									
P. adstrictus	1	12	11	11	7	7	1	10	10	11	22
	2	0	2	0	1	8	1	4	2	0	4
P. pensylvanicus	1	0	0	0	2	5	7	3	7	5	0
	2	2	6	5	3	1	3	0	2	7	1

Effects of Some Abiotic Factors

Under the warmer (18 C) conditions of the laboratory, 30 females laid 1.8 times more eggs per individual than did 10 females under conditions approximating field conditions.

For oviposition, the females used mostly the wettest soil conditions (labelled 'E' in Fig. 7). They laid eggs in various granular materials such as sifted forest soil, peat moss, and sand (more than 1.1 eggs per female per day under laboratory conditions), but avoided laying on non-granular substrates such as paper (less than 0.05 eggs per female per day under laboratory conditions). The loosest soil conditions were most used for oviposition (Fig. 8).

4.1.3.3. *Egg Stage*. The viability of eggs was high. In 1968, in spite of mite and fungus problems, 60% of 1201 eggs hatched; but if disease factors are eliminated, 90% to 100% of several hundred eggs hatched.

The time required for development varied with temperature. Under constant conditions of temperature (20 C), 11 eggs required 10.6 ± 0.8 days to develop; under conditions approximating field temperatures (about 7 C), 15 eggs required 39.5 ± 1 days to develop. High temperatures affected egg mortality, as at a temperature of more than 25 C, more than 50% of the eggs died, but eight eggs exposed to a temperature of -5 C for 24 hours were not damaged.

Moisture plays an important role as the eggs absorb water from the soil. Eggs were significantly heavier just before hatching (maximum length x maximum width just before hatching was 1.57 ± 0.06 mm^2 while just after oviposition it was 1.44 ± 0.05 mm^2). Excess or lack of moisture killed the eggs by drowning (10 eggs tested), or by desiccation (five eggs tested). Within the range of studied conditions (from 'B' to 'E' of Section 3.3.5.1.).

the development was successful.

4.1.3.4. *Larvae*. From 1968 pitfall trapping data, the average emergence dates of the first, second, and third instar larvae were on June 13, June 23, and July 5 respectively. So the time required from the first to second instar was 11.5 days, and from second to third instar was 14.1 days. In the laboratory under constant temperature conditions (20 C) it took seven to eight days from first to second instar, and eight to nine days from second to third. Thus average field conditions were probably less than 20 C. Total larval development took 28.3 days in the laboratory.

4.1.3.5. *Pupae*. From pitfall data in 1969, the peak of emergence of the third instar larvae was on July 23, and the peak of emergence of the teneral adults was on September 30 (total interval of 70 days). Ten specimens reared at 20 C passed 45% of the inactive period from the third instar larvae (when quiescent) to partly tanned teneral adults, as pupae. Thus 45% of 70 days suggests a pupal period of about 31 days.

4.1.4. Population Fluctuations from 1967 to 1970

As shown in Fig. 9, the population of *P. pensylvanicus* probably changed little during the entire study period. The small variations shown in the figure are not significant as the method of pitfall trapping permits only very crude estimates of population.

4.1.5. Morphology of *P. pensylvanicus*

4.1.5.1. *Adults*. Description of the external morphology of the adults as well as of the male genitalia was made by Lindroth (1966). However, the female internal reproductive tract also shows interesting characteristics.

The internal female reproductive tract is shown in Fig. 11. On the

Fig. 11. Dorsal view of the female internal reproductive system (ovaries, part of vagina, and ovipositor omitted).

a) *P. adstrictus*

p) *P. pensylvanicus*

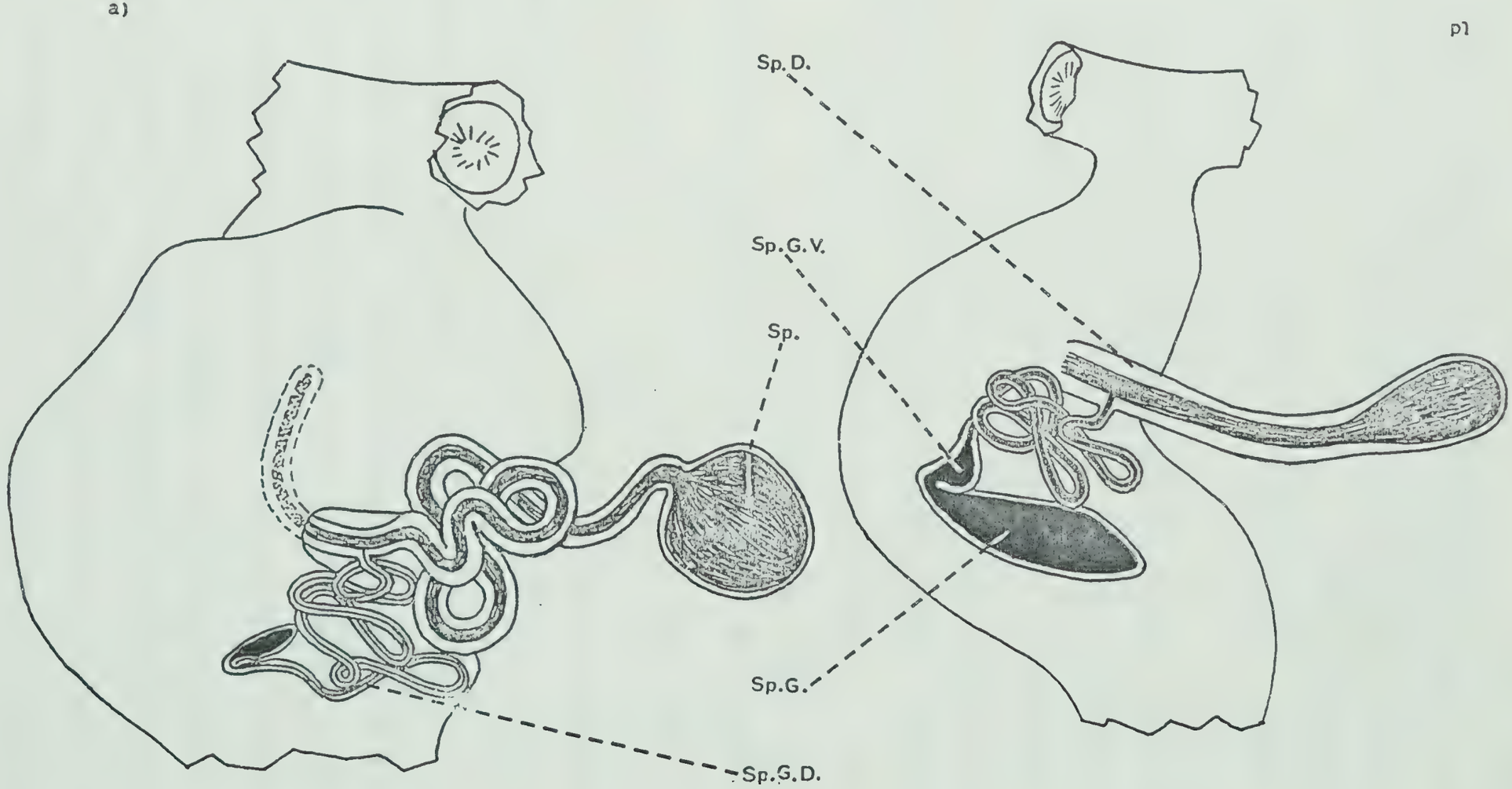
Sp. - spermatheca

Sp. D. - spermathecal duct

Sp. G. D. - spermathecal gland duct

Sp. G. V. - spermathecal gland vesicle

Sp. G. - - spermathecal gland


a)
p)
Sp.D.
Sp.G.V.
Sp.
Sp.G.
Sp.G.D.

dorsum of the *bursa copulatrix* is the apparent opening to the spermathecal duct. This duct is short and wide. The apical reservoir is small, and its inner diameter is about three times larger than the inner diameter of the spermathecal duct. The long duct of the spermathecal gland originates on the side of the spermathecal duct about one-fifth of its length from the bursal opening. The inner diameter of this convoluted tube is half the inner diameter of the spermathecal duct. This duct ends in a small vesicle which is followed immediately by a very large securiform spermathecal gland.

4.1.5.2. *Description of the Larvae.* The generic characteristics are as described by Van Emden (1942).

Third Instar Larva

Description - Characteristics of *Pterostichus* plus the following.

Head Width. 1.4 to 1.7 mm.

Color. Following rufo-testaceous: head, mandibles, mentum, and head appendages. Terga of thorax, prosternum, and legs testaceous. Abdominal sternites and pleurites very pale testaceous.

Chaetotaxy. Tergites and sternites with numerous irregular small setae. Innermost basal setae of mesonotum about 0.2 to 0.4 times as long as external basal setae. Nine setae on urogomphi; and five setae on abdominal epipleurites.

Thorax. Pronotum about 1.5 times as wide as long; meso- and metanotum twice as wide as long.

Abdomen. Terga at base twice as wide as long, and at apex 1.5 times as wide as long. Urogomphi moderate in length and slightly curved inward at apex.

Microsculpture. Cells on frons more convex, thus head dull.

Second Instar Larva

Description - Similar to third instar, differing in the following.

Head Width. 1.0 to 1.2 mm.

Chaetotaxy. Number of irregular small setae less abundant. Innermost basal setae of mesonotum about 0.1 to 0.2 times as long as external setae.

First Instar Larva

Description - Differs from the two preceding instars in the following.

Head Width. 0.6 to 0.7 mm.

Chaetotaxy. No irregular small setae. Innermost basal setae of meso- and metanotum absent or barely visible. Five setae on urogomphi, two setae on abdominal ventrites and postventrites; no setae on hypopleurites. Abdominal epipleurites with one long seta (rarely a second very small one visible).

4.2. *Pterostichus adstrictus*

4.2.1. Geographical Distribution

As a circumpolar species, *P. adstrictus* is one of the most widely distributed species of carabids in the world. It has been reported from Iceland, northern British Isles, Ireland, Faeroes, Denmark, westward through northern Russia, Siberia, northern Mongolia to Kamtschatka (Lindroth, 1945). In America, it has been found south of the tree line transcontinentally from Newfoundland to Attu in Alaska, and as far south as southern Canada (London, Ontario) and in high altitudes along the western mountain chain to California and along the eastern Appalachians in New England (Lindroth, 1966).

4.2.2. Habitat

Specimens of this species may be expected in woodland as well as in open land (including cultivated fields). Specimens are found on the coastal

tundra of southern Labrador, Kodiak and Aleutians Islands, but not on the more northern tundra (Lindroth, 1966). These beetles are found in moist to dry soil, and often in rotten logs.

The preferred habitat varies with the region. In coastal regions specimens are relatively independent of the forest cover, while in the interior, as in Alberta, they are found mostly in dense vegetation: tall grassland to forest vegetation (Frank, 1971). In Norway, Lindroth (1945) observed that they were most abundant in moderately moist land. In these regions, these beetles seemed synanthropic as they do best in habitats affected by man, such as lumbered and cultivated lands. In Alberta they do best in the forest habitat even in its darkest parts (white spruce forest), or in wet conditions as at the edge of marshes. On its southern-most limit (at sea level in eastern Canada near Montreal) individuals are restricted to forest litter on north-facing slopes in dark and cool conditions.

The adult stage may be expected in most litter habitats. In the spring, individuals are often under bark where they oviposit (it is not certain that they oviposit in the litter because no first instar larvae were found there). Only two eggs were found, and these were in moist decayed wood. The larvae were collected commonly in decayed wood and under leaves. However, the first and second instar larvae were found mostly in decayed logs while the third instar occurred quite commonly in the leaf litter as well as in the old logs. The pupae were commonly collected in decayed wood in moist cool situations.

4.2.3. Ecological Characteristics

4.2.3.1. *Cycle.* In early spring the adults (some of which had emerged

the previous fall, and some of which were more than a year old) become active, and seek food and mates. The period of high activity starts to decrease from the end of May or early June, and the beetles enter a summer quiescent period. Oviposition occurs during the period of high activity from early May until the last week of June when most females are spent (before the summer quiescent period).

By mid-June, eggs start to hatch. The young larvae develop rapidly and by mid-August and September the new adults emerge from the pupal cells after their cuticles are almost completely tanned. During the emergence period, both old and new adults are active in the litter. From September to November (depending on the year), the adults become inactive and overwinter either singly or in aggregations in logs or under stones.

4.2.3.2. *Adults.*

(a) *Relative activity of each sex and age-group.* Not much can be said of the unmarked population during the fall as adults were mostly quiescent by that time, and thus very few captures were made. From data in Table 2, the specimens of the old generation were probably twice as active as those of the new generation, and the males were probably as active as the females in both generations.

In the spring, more can be said of the unmarked population because more unmarked specimens were collected. The adult density was estimated at 0.48 specimens per square meter (based on marked and released specimens in a similar age ratio to that of the unmarked population. Calculations are shown in Section 3.2.3.). As the males were only slightly more active than the females, it is probable that the unmarked females were rare relative to the unmarked males. During this period, the marked old and new generation specimens showed a very high female activity suggesting a very high male

mortality as the spring activity of the released mixed adults was similar between sexes.

(b) *Activity as inferred from the capture rate.*

Seasonal

The seasonal activity, in its general outline, was similar from year to year (as shown for 1969 in Fig. 3). As the litter temperature increased in early spring, adults started to wander. During May, the activity remained very high. Then, from the end of May or the beginning of June, the activity decreased until the end of June when very few adults were captured. By August, as the new adults emerged, both old and new generation adults became active again. The activity again decreased between the end of September and the beginning of November. After this period, the beetles were ready to overwinter. Females were generally as active as the males except in very early spring when a higher proportion of males was trapped. By the end of May or early June a higher proportion of females was trapped.

Daily

Adults show a greater rate of activity at night (as an example, see Fig. 4).

(c) *Mating.* Mating was observed three times in the field (though the adults were relatively rare) during May and early June in 1969 (in 1967 and 1968, no matings were observed in the pitfall traps). The time required for copulation was about 12 hours for most pairs observed in the laboratory. Mating was observed both during the day and at night in the laboratory.

When males were put with females of the same species, I observed six copulations in 75 trials in less than 48 hours. But no copulation was observed with females of *P. pensylvanicus*.

No males were especially attracted to virgin females of their own

species when tested for volatile pheromones in the apparatus described in Fig. 2 (Table 5).

(d) *Oviposition.*

Cycle

Females oviposited starting in early May and ending in the last week of June (Fig. 5). The end of oviposition occurred at rather similar times from 1968 to 1970.

Ovaries Analysis

The average egg content per female was 13.6. This is lower than the average number of eggs (32) laid by a female under conditions approximating field temperatures. The number of eggs per female varied as a function of time (Fig. 6). In very early spring no eggs were observed. In May the average egg production was very high and in June the average decreased. By the end of June most of the females dissected were spent.

The females dissected were either old females or young ones which had emerged the previous fall. The old females show well-developed *corpora lutea* in early May, while the young ones show none, or very small ones. In 1970, four of 18 females were more than a year old.

Patterns of Egg Production

Freshly caught females laid most of their eggs within two days of their capture as shown in Table 6. The average production per female in a day was 1.15 eggs (average based on the time taken to lay 90% of eggs) under temperature conditions approximating field conditions (thus only 2.3 eggs should be laid in two days). But the average number of eggs laid during this peak period of two days was 12.4 under temperature conditions approximating field conditions. Moreover, the average was similar to the average number of mature eggs per dissected female (13.6). Thus, during a peak

period, a female probably lays the whole egg content of her abdomen.

Effect of Some Abiotic Factors

Under the warmer conditions (about 18 C) of the laboratory, 30 females laid 3.16 more eggs than did 10 females under conditions approximating field conditions.

Eggs were laid in moist to wet soil conditions, but not in dry soil (Fig. 7). The eggs were laid in various granular materials such as sifted forest soil, peat moss, and sand (more than three eggs per female per day under laboratory conditions), but not on non-granular substrates such as absorbent paper.

4.2.3.3. *Egg Stage*. Under suitable conditions of temperature (less than 20 C) and moisture, 90% to 100% of eggs hatched.

The egg development is similar between the individuals as 75 eggs at 20 C took 9.6 ± 0.7 days to hatch. Under temperature conditions approximating field conditions (on average 7 C) 20 eggs completed their development in 36 ± 1.1 days. Under high temperature conditions (over 25 C) more than 50% of the eggs were lost, but under very low temperatures (-5 C) for 24 hours no eggs were damaged.

During their development, eggs absorb water from the substrate, as the egg size just prior to hatching is significantly larger than the size just after being laid (maximum length by maximum width of nine eggs was 1.48 ± 0.03 mm^2 just after being laid, and 1.64 ± 0.05 mm^2 just before hatching). Inside the range of moisture 'B' to 'E' (Section 3.3.5.1.) the eggs developed well, but moisture condition 'A' killed them rapidly through desiccation. Finally, wet conditions killed the eggs by drowning.

4.2.3.4. *Larvae*. The average emergence date of the larvae was estimated from the 1968 pitfall trapping data. Thus, the first, second, and third instar larvae had emerged on average by June 10, June 18 and June 27 respectively (this varied from year to year). The time between the first and second instar was probably 8.0 days, and between the second and third was probably 9.0 days. Under laboratory conditions at 20 C individuals of the first instar reached the second instar in eight days, and individuals of the second instar reached the third instar in eight to nine days. Thus, it is probable that field temperatures averaged 20 C. Total larval development at 20 C required 27.7 days.

4.2.3.5. *Pupae*. From pitfall data of 1969, the larvae started to be inactive on July 23, and the emergence peak of new adults was on August 23. Probably 45% of this period was spent in the pupal stage (from laboratory data). Thus, it is probable that the pupae require an average of 14 days for development. Under laboratory conditions (20 C) the pupae developed in eight days. Thus, average field temperature conditions were probably lower than 20 C.

4.2.4. Population Fluctuations from 1967 to 1970

The *P. adstrictus* population probably decreased in 1969 and remained at the same level for 1970 (Fig. 9). Other small variations were probably meaningless as pitfall trapping provides only very rough estimates of population size.

4.2.5. Morphology of *P. adstrictus*

4.2.5.1. *Adults*. Description of the external morphology of the adults as well as of the male genitalia was made by Lindroth (1966).

Characteristics of the female reproductive tract are presented below.

The internal female reproductive tract is shown in Fig. 11. On the ventral side of the *bursa copulatrix* is the opening of the spermathecal duct. The spermathecal duct is long, wide, and convoluted. It ends in a large apical reservoir, oviform in shape. Its internal diameter is eight to nine times wider than the inner diameter of the spermathecal duct. On the side of the spermathecal duct near its opening, at about one-fifth of its total length, the very long and convoluted duct of the spermathecal gland originates. The inner diameter of this duct is about one-third of the inner diameter of the spermathecal duct. This duct ends in a very small vesicle which is followed immediately by a small securiform spermathecal gland.

4.2.5.2. *Description of the Larvae.* The generic characteristics are as described by Van Emden (1942).

Third Instar Larva

Description - Characteristics of *Pterostichus* plus the following.

Head Width. 1.6 to 1.9 mm.

Color. Following rufous: head, mandibles, mentum, disc of pronotum, and prosternum; head appendages slightly paler. Meso- and metatergum, and discs of abdominal terga rufo-testaceous or testaceous. Legs testaceous. Lateral and ventral sclerites, uropod, and urogomphi very pale testaceous. Remaining membranous areas white.

Chaetotaxy. Tergites and sternites with numerous irregular small setae. Innermost basal setae of mesonotum about 0.75 times as long as lateral basal ones. Nine setae on urogomphi, and five to seven setae on abdominal epipleurites.

Head. Slightly wider than long. Nasale slightly emarginate, denticulate, and angles each with sharp tooth.

Thorax. Pronotum about 1.5 times as wide as long; meso- and metanotum twice as wide as long.

Abdomen. Terga at base twice as wide as long, and at apex 1.5 times as wide as long. Urogomphi moderate in length and slightly curved inward at apex.

Microsculpture. Patchy and little convex cells on frons.

Second Instar Larva

Description - Similar to third instar, differing in the following.

Head Width. 1.0 to 1.3 mm.

Chaetotaxy. Irregular small setae less abundant. Innermost basal setae of mesonotum about 0.5 times as long as external basal setae.

First Instar Larva

Description - Differs from the two preceding instars in the following.

Head Width. 0.6 to 0.8 mm.

Chaetotaxy. No irregular small setae. Innermost basal setae of the mesonotum about 0.3 to 0.5 as long as external basal setae. Five setae on urogomphi; two setae on abdominal ventrites and postventrites; no setae on hypopleurites. Abdominal epipleurites with two setae; smaller one about 0.5 times as long as other.

5. Comparison of the Ecological and Morphological Characteristics of *P. adstrictus* and *P. pensylvanicus*

5.1. Geographical Distribution

Both species are widely distributed in the middle and northern latitudes. *P. pensylvanicus*, however, shows a more southern distribution (northern limit being the southern boreal forest, and the southern limit in northern New England at low altitudes) and a more eastern distribution. It enters as far as central British Columbia, its westernmost limit.

5.2. Habitat

Specimens of both species can live together in the forest. *P. adstrictus* is more eurytopic as its tolerance to variation in abiotic components is greater. This was illustrated in some of the experiments, and by the habitats where the adults have been collected. Adults live in dry to very moist habitats (field and willow habitats), and in cool to very warm habitats (spruce bogs and oat fields). *P. pensylvanicus* is generally more stenotopic. This was illustrated first by some laboratory experiments and by the habitats where the adults have been collected. Its populations seem to be restricted generally to forest habitats, and in Alberta the adults were most abundantly collected in naturally well-drained and open aspen forest. Moreover, in Alberta the species is not represented in other forest litter habitats where adults of *P. adstrictus* occur. Even in the middle of their ranges, populations of *P. pensylvanicus* are more restricted in their habitats than are populations of *P. adstrictus*, as the former do not occur outside forest litter habitats.

The adults of *P. adstrictus* live in the leaf litter and, in the spring, mostly in decayed wood where they oviposit. *P. pensylvanicus* adults were not found in logs. The oviposition, it is assumed, is entirely restricted to habitats under the leaf litter.

The first and second instar larvae of *P. adstrictus* live mostly in logs; the third instar larvae are found either in logs or below the leaf litter.

The pupae of *P. adstrictus* were found in logs, but those of *P. pensylvanicus* were not. It is assumed that the pupae of *P. pensylvanicus* occur only beneath the surface of the soil below the leaf litter.

5.3. Ecology

5.3.1. Cycle

The life cycle for both species is very similar and varies only in details.

5.3.2. Adults

5.3.2.1. *Relative activity of each sex and age-group.* During the fall, adults of *P. pensylvanicus* were active until freezing by November (Fig. 3), and thus they showed an activity rate three to four times as high as those of *P. adstrictus*. In the old generation of *P. adstrictus*, and the new generation of both species, the females were probably as active as the males, but in the old generation of *P. pensylvanicus* the females were less active than the males. In both species, the old generation specimens were more active than the new adults.

In the spring (Fig. 3), adults of both species were probably equally

active (ratios of captured to released specimens were 0.42 and 0.38 for *P. adstrictus* and *P. pensylvanicus* respectively). Both old and new generation males were rarely caught. It is assumed that the big difference in activity was due to a much higher death rate in males in winter, because the released mixed-generation adults showed almost equal activity in males and females. The adult spring density of each species was: *P. adstrictus* - 0.48 specimen per square meter, and *P. pensylvanicus* - 0.61 specimen per square meter. Many of the results obtained through marking-recapture were common to both species. The released specimens of the old generation were apparently more active than the released specimens of the new generation in the fall. The activity of the males relative to females was similar in all released groups over each of the periods studied. However, because more of the males of the released old generation of *P. pensylvanicus* were captured, it is probable that they were more active than the females. The mortality during the winter for the males was very high in the old and new generations (less severely in *P. adstrictus*). This high mortality may be due to various factors, but I believe that the very light snow cover in the winter of 1969-70 probably affected the increase in mortality rate.

5.3.2.2. *Activity cycle as inferred from the capture rate.* The seasonal activity cycles of both species were typical of what is known as 'spring species' (Larsson, 1938). This cycle consisted of a spring peak of activity reached at the same time for both species. This was followed in July by a quiescent period when few specimens were collected. In later summer or early fall, there was a new peak of teneral activity (linked with teneral emergence). This second peak was not necessarily reached at the same time by both species. Moreover, during my stay at George Lake, I observed that *P. pensylvanicus*

teneral adults appeared later than those of *P. adstrictus*. The general outline of this cycle varied slightly from year to year (both peaks were reached at different dates each year); but the timing of the quiescent period was rather constant (the end of June).

This suggests that the spring and fall peaks are not started by a given day length effect (though day length may play a preparing role). The summer quiescent period is probably started through day length effect (as shown by Thiele [1969] in other carabids such as *Nebria brevicollis*). Finally, the emergence period is probably controlled by the effect of temperature on the development rate. The end of the emergence and fall activity periods may be stopped abruptly by an early winter (1970-71 winter) or perhaps by day length as adults kept in the laboratory were inactive under the short day lengths of November.

The circadian rhythm of both species in summer is similar as both gradually approach the highest activity rate at night. However, in *P. pensylvanicus* (unfortunately no data were available for *P. adstrictus*) when the nights were cold (less than 0 C in the fall) most specimens were caught during the day. The cause of this last change is not clear, but cold nights may offer a possible explanation because, as Thiele (1968b) suggests, in some species rhythm may be under temperature control.

5.3.2.3. *Mating*. Mating occurred from May until the first week of June. However, specimens of *P. pensylvanicus* were often observed mating in the fall (it is probably so for *P. adstrictus* but was not observed). Copulation usually lasted for 12 hours.

Males of both species mate with females of their own species. There must be a mechanism involved in female recognition. Volatile pheromones

are apparently not emitted. So identification probably takes place at very short distances, by other means.

5.3.2.4. *Oviposition.*

Cycle

Oviposition extends over one long period starting in early May and continuing until the end of June. The end of oviposition is probably under day length control, as it ended at the same time each year during this study. The beginning of oviposition is slightly variable from year to year. Females which mate in the fall do not oviposit as a period of short day length or cold temperature, or both, is probably necessary for the development of ovaries (Thiele, 1968b).

Analysis of Ovaries

The average number of eggs per dissected female was slightly different between the species. The average per female of *P. adstrictus* was 1.38 times higher than the average per female of *P. pensylvanicus*. The average number did not show the real oviposition potential for females through the season as each species probably lays 2.2 to 2.3 times their average egg content at field temperatures.

The average number of eggs in both species varied throughout the season. During May, the average increased (females of *P. adstrictus* reached a higher average early in May in 1968). After mid-June the average number per female decreased rapidly, and by the end of June most females were spent.

As shown through the development of *corpora lutea* in dissected females, 30% of *P. adstrictus* and 50% of *P. pensylvanicus* females were at least more than a year old.

Pattern of Egg Production

Females of both species, when brought to the laboratory, tended to lay most of their eggs within three days. Thereafter, only a few eggs were laid. This suggests that in the field the females may lay eggs in batches.

Effects of Some Abiotic Factors

With warmer temperatures females lay more eggs, but the effect varies with the species. Under conditions approximating field conditions *P. adstrictus* females laid 1.5 times as many eggs as *P. pensylvanicus* females, while at laboratory temperatures *P. adstrictus* females laid 2.5 times as many eggs as *P. pensylvanicus* females.

Females of both species avoid ovipositing in dry soil (such as air dried peat moss). *P. adstrictus* females oviposited indiscriminately on slightly moist to very moist soil, while those of *P. pensylvanicus* oviposited mostly in very moist soil (the ranges 'D' and 'E').

Oviposition is much reduced when soils are hard to penetrate due to compression. In *P. pensylvanicus*, 76% of eggs were found in the loosest soil conditions (ranges 'A' and 'B'), while in *P. adstrictus*, 94% of eggs were laid similarly over the ranges 'A' through 'D'.

Females of neither species oviposit on non-granular substances.

Females probably lay eggs in batches corresponding in size to their abdomen content. Taking into account the oviposition period, and the oviposition rate for each species, females may lay an average of 2.2 batches of eggs per season. This pattern is possibly adaptive for a scarcity of suitable oviposition sites.

5.3.3. Eggs

Under moist conditions (moistures 'B' to 'E'), and cool temperatures

(<20 C), a very high percentage (90% to 100%) of the eggs for both species hatched as opposed to 32% reported by Penney (1965, 1967) for a related species.

The temperature affects the development rate. As the temperature increased, the development rate increased in both species. Under both laboratory and field conditions, *P. adstrictus* eggs required less time to develop (one day less in warm conditions, and 3.5 days less in cool conditions).

Lack of moisture killed the eggs by desiccation, and an excess killed by drowning in both species. The eggs absorbed water from the soil. Under the conditions of moisture 'B' to 'E', eggs developed normally.

5.3.4. Larvae

The larval cycle was similar in the two species. The larval stage extended from mid-June to August or September. The peak of each instar varied slightly from year to year, but in each year, at least the third instar of *P. adstrictus* was earlier than that of *P. pensylvanicus*. Thus the *P. adstrictus* cycle was apparently shorter.

In the laboratory at 20 C the larval cycle of both species was about the same (the average difference was half a day). Thus, it would be reasonable to postulate that the differences observed were probably a result of temperature differences in the different habitats of the species. Thus *P. adstrictus* larvae probably lived in a generally warmer habitat than did those of *P. pensylvanicus*.

5.3.5. Pupae

From 1969 data it is suggested (from extrapolation from laboratory data) that individuals of *P. adstrictus* developed on average in 14 days, and that individuals of *P. pensylvanicus* developed in 31 days. In the

laboratory at 20 C the total length of the pupal stage was similar in the two species (eight days), so it is reasonable to assume that in 1969 the observed difference between the time required for pupal development in each of the species was due to average temperature conditions of the habitat chosen by each species. Thus the pupae of *P. adstrictus* were probably living in a generally warmer habitat.

Eclosion of the pupae of both species occurred in the fall. In new females of both species the ovaries remained immature (Thiele, 1968b) as recently fertilized females of *P. pensylvanicus* did not lay eggs before the winter. I do not know if the sperm kept in the spermatheca survive the winter period; however, very few matings were observed each spring suggesting that the females may still be fertilized from the previous fall.

5.4. Morphology

5.4.1. Morphological Characteristics of the Adults

External characteristics

As the adults have been described (Lindroth, 1966), I will just point out characteristics by which both species differ at George Lake.

In *P. adstrictus*, the hind angles of the pronotum are rectangular, the pronotum basal impressions are densely punctate, the elytral foveae (especially the last one) are very expanded, and the elytra are longer relative to the pronotum. Thus the equation 0.265 x (elytron length) - 0.705 x (pronotum length) is greater than -0.198. It was found that the ratio of length of pronotum to length of pronotum at its widest point, as proposed by Barlow et al. (1969), is very subjective and unreliable, as the position of the point on the pronotal margin where it is the widest is very difficult to situate. In this area the margin is nearly straight. Thus the position of the point

is subjective, and the slight difference between these two species makes the discriminant function unreliable.

In *P. pensylvanicus* the hind angles of the pronotum are obtuse, the pronotum basal impressions are less or not punctate, the elytral foveae are slightly expanded, and the elytra are shorter relative to the pronotum. Thus the equation 0.265 X (elytron length) - 0.705 X (pronotum length) is smaller than -0.198.

Internal characteristics

Besides the adult characteristics pointed out by Lindroth (1966), the most striking and probably most significant characteristics may be obtained from the analysis of the internal female genitalia (Fig. 11). I found no significant interspecific differences in the ovaries, oviducts, vagina, and styli, but the spermathecal apparatus is strikingly different. In *P. pensylvanicus* the spermathecal duct penetrates the vagina tissue dorsally, but in *P. adstrictus* it penetrates ventrally. (If the vaginal tissue is dissolved in KOH, the spermathecal duct of the two species opens ventrally near the common oviduct.) Other differences are the sperm reservoir which in *P. adstrictus* is extremely large, and the spermathecal gland and its vesicle are extremely small, whereas in *P. pensylvanicus* the sperm reservoir is rather small and the spermathecal gland and its vesicle are extremely large. The other differences noticed, such as duct length and diameter, are constant.

5.4.2. Morphological Characteristics of the Larvae

The instars of the larvae are recognized as follows. The first instar larva is characterized by the presence of egg bursters on the frons, five setae on the urogomphi, no membranous area near the middle of the maxillary stipes, the cervical keel is short and not curved ventro-laterally, and the

head width is less than 0.7 mm. The second and third instars show no egg bursters, have nine setae on the urogomphi, there is a membranous area near the middle of the maxillary stipes, the cervical grooves are curved ventrolaterally to the eye level, and the head is wider, at least 1.0 mm. The second instar differs from the third with its smaller head (less than 1.4 mm), and by the less developed irregular setae on the sclerites.

The larvae of the two species are distinguished from one another as follows:

1. The first instar larvae of *P. adstrictus* show two well-developed setae on the epipleurites, and the innermost basal setae of the meso- and metanotum are present (at least 0.3 to 0.5 times the size of the lateral setae). In *P. pensylvanicus* first instar larvae only one seta is present on the epipleurites (at most a second very small one may be present), and the innermost basal setae of the meso- and metanotum are absent (or barely visible).

2. In the second instar larvae of *P. adstrictus*, the innermost basal setae of the mesonotum are about 0.5 times as long as the external basal setae, while in *P. pensylvanicus* they are 0.1 to 0.2 times as long as the basal setae.

3. In the third instar of *P. adstrictus*, the innermost basal setae of the mesonotum are at least 0.75 times as long as the external basal setae, while in *P. pensylvanicus* they are less than 0.4 times as long as the external basal setae.

6. General Discussion

6.1. Introduction

The data obtained in the previous sections not only permit us to know about biological similarities and differences between these two species, but also, they may throw some light on the basic principles of their dynamics, their present distribution, and their evolution.

Individuals and groups of a species are limited by the pressures of their environment (such as other species, food, and numerous abiotic factors). These pressures act with intensities which may vary with time, thus affecting positively or negatively the success of individuals and of populations. Each species has its own potential for increase, but what are the factors which may affect the net rate of increase? The curtailing factors are numerous, and they may partially explain population variation in time. So, for the survival of a population, the potential for increase should be in relative equilibrium with the average effect of these factors. Otherwise, the population might be eliminated through outbreaks or crashes. Thus, living organisms must adjust to environmental factors; and such processes of adjusting cause species formation, species evolution, and species extinction.

In the following sections, attempts will be made to explain some of the factors involved in the observed population fluctuations, and differences in their present distributions; some of the principles involved in the reproductive isolation; the adaptive significance of the various biological characteristics; and the relationship and the past history of each species.

6.2. Attempt to Explain Differences in Population Fluctuations

6.2.1. Introduction

In the past four years the populations of both species at George Lake have undergone changes in their size as shown in Fig. 9. The data suggest that the *P. pensylvanicus* population remained relatively stable, while in 1967 and 1968 the *P. adstrictus* population was much larger than in the following years.

What were the main factors involved in producing these changes? Only some of the possible biotic and abiotic factors were investigated (excluding catastrophes). But the analyses of the data obtained in the laboratory and in the field apparently explain the observed changes over the four years studied. Of course, no final conclusions can be drawn from laboratory data about phenomena occurring in the field, but the suggestions proposed are given as a beginning point for further research in population dynamics of these species.

6.2.2. Factors Probably Involved in Controlling Populations

The Biotic Factors

The biotic factors influence population size, but their effect was not very evident in the course of the research for the following reasons:

1. I think that competition for food is of secondary importance. Thiele (1968b), with related species of *Pterostichus*, found some competition effects in overcrowded conditions when the food quantity was minimal. But in the field, such conditions do not exist as the adult density is usually less than one per square meter and as the food potential of that unit area far exceeds the requirements of the beetles (to rear one

specimen from egg to adult at 20 C requires only 2.5 *Tenebrio* larvae, and to maintain one adult female requires only three *Tenebrio* larvae). Moreover, in the enclosed area where the population was doubled by the introduction of marked specimens, there was no sign of starvation—the percentage of trapped specimens with enlarged abdomens due to fat was similar to that outside the enclosed area.

2. Interaction with other species of insects, or interaction between specimens of the same species, is apparently not important. This was suggested in the laboratory work under crowded conditions where specimens were neither attracted nor repelled by other specimens. In the field, on the other hand, with small plastic pitfall traps, the chance of capturing two specimens in a day is very small, so the chance that the paths of two beetles would cross simultaneously in the leaf litter is probably very small indeed (assuming no scent-trails), and would probably have very little consequence at any rate. The same may be applied to the larvae which live in a three dimensional habitat and isolate themselves in time, thereby making encounter even rarer.

3. Predation varies from year to year with the fluctuations of predator populations (predators such as *Clethrionomys gapperi* Vigors, *Microtus pennsylvanicus* Ord., *Bonasa umbellus* L., *Microsorex hoyi* Baird) but it is thought to have very little effect on these species, as grouse and shrews are scarce per unit area, and as mice do not especially feed on these species (analyzed stomachs contained no evidence for it). Possibly spiders eat ground beetles (Exline, 1934; Leech, 1971), but the evidence from pitfall trapping shows the opposite as I saw numerous spiders being eaten by carabids.

4. Parasitism and disease at George Lake during the study period appeared

to play a minor role in mortality of larvae and adults. Less than 5% of females dissected at the end of June were under the influence of a disease or, in May, were attacked by gordian worms. Finally, less than 5% of the pupae found in 1969 were attacked by fungi.

The Abiotic Factors

The abiotic factors apparently played a leading role in affecting the population size from year to year in the course of the study.

To demonstrate some of the probable causes of these fluctuations, various data related to behaviour and reactions to environmental conditions for various stages are summarized in Table 8. Each of these characteristics is affected by the qualities of the chosen habitat for each stage of each species.

Adults of *P. adstrictus* occur in the litter as well as in logs, but their immature stages are mostly restricted to logs. All stages of *P. pensylvanicus* occur in the leaf litter or under it in the soil. The effect of these chosen habitats on each stage of each species is discussed.

1. Survival of eggs is dependent on the physical characteristics (mostly moisture) of the oviposition site. Since females of *P. adstrictus* do not necessarily choose the wettest habitat available, and since they oviposit in logs which are subject to rapid drying, eggs may be killed in a drought. But females of *P. pensylvanicus* tend to choose wet conditions in soil below the leaf litter. This habitat is less subject to rapid drying, and consequently egg mortality due to desiccation may be lower. In wetter conditions, *P. adstrictus* populations may be more successful than those of *P. pensylvanicus* because the females of *P. adstrictus* have a higher oviposition rate.
2. The larval mortality may not vary greatly from dry to wet conditions

Table 8. Summary for each developmental stage of behavioural and physiological characteristics for *P. adstrictus* and *P. pensylvanicus*.

Stage	Species	
	P. pensylvanicus	*P. adstrictus*
	Characteristics	
Adult females	- oviposit under litter in soil	- oviposit in logs
	- oviposit on wettest substrates	- oviposit in various moist substrates
	- start ovipositing by mid-May	- start to oviposit earlier
	- lay 0.7 times as many eggs as *P. adstrictus*	- lay 1.5 times more eggs than *P. pensylvanicus*
	- lay on granular substrates	- as for *P. pensylvanicus*
Eggs	- must absorb water from substrate	- *id.*
	- low temperature for short periods have no effect	- *id.*
	- high temperatures increase mortality	- *id.*
	- hatch later than *P. adstrictus* under similar conditions	- hatch earlier than *P. pensylvanicus* under similar conditions

(Cont'd)

Table 8 (Cont'd)

Stage	Species	
	P. pensylvanicus	*P. adstrictus*
	Characteristics	
Larvae	- Move easily in gradients of moisture, R.H., and temperature (Paarman, 1967)	- as for *P. pensylvanicus*
	- develop in 28 days at 20 C	- *id.*
	- develop slower in the field than *P. adstrictus*	- develop faster in the field than *P. pensylvanicus*
	- very cannibalistic	- as for *P. pensylvanicus*
Pupae	- killed by low R.H.	- *id.*
	- not killed by low substrate moisture	- *id.*
	- develop in 8 days at 20 C	- *id.*
	- often develop slower in the field than *P. adstrictus*	- often develop faster in the field than *P. pensylvanicus*
	- cannot overwinter	- as for *P. pensylvanicus*
Teneral	- can overwinter	*id.*
	- mate, but do not lay eggs	*id.*

because the larvae respond to moisture conditions by moving to the region most suitable for them (Paarman, 1966). The main difference between dry and wet conditions is that the dry conditions may accelerate the larval development rate as higher temperatures may be reached. In the laboratory, the larvae of both species take nearly the same time to develop, so any difference observed in the field is probably due to differences in average temperatures of the chosen habitat. So, in dry conditions both species may develop rapidly; but, in wetter conditions, larvae of *P. adstrictus* develop faster than larvae of *P. pensylvanicus* because their chosen microhabitat in logs may be warmer than the soil below the litter.

3. In the pupal stage the only important variable of those studied is the temperature because, in the laboratory, both species developed at the same rate. Again, the average temperature is probably most affected by the chosen microhabitat. So, in wet periods, pupae of *P. adstrictus* may develop faster in the logs than those of *P. pensylvanicus;* and, in dry periods, both may develop rapidly.

All these stages show different mortality rates which may be affected by diseases, especially in wet conditions, or by desiccation. If the effects of the climate of one period are added to the effects of the next, these interacting factors could favour or suppress one or both of the species in similar or different ways. The final result is the number of adults surviving for reproduction in the following season.

The probable climatic effects on the populations are summarized in Table 9 and Fig. 10. The expected data in Figure 10 appear to fit relatively well with the observed changes in populations at George Lake (Fig. 9).

Table 9. The probable effect of weather on each developmental stage of *P. adstrictus* and *P. pensylvanicus* during spring, early summer, and late summer.

Period	Condition	Species	
		P. pensylvanicus	*P. adstrictus*
		Effects	
Spring	Dry	- low egg mortality - fast development	- high egg mortality - faster development than *P. pensylvanicus*
	Wet	- low egg mortality - slow development	- as for *P. pensylvanicus* - slow development, but faster than *P. pensylvanicus*
Early summer	Dry	- larval mortality rate low - development fast	- as for *P. pensylvanicus* - development faster than for *P. pensylvanicus*
	Wet	- larval mortality rate low - development much slower than *P. adstrictus*	- as for *P. pensylvanicus* - development slow
Late summer	Dry	- pupal mortality low - development fast	- as for *P. pensylvanicus* - development faster than for *P. pensylvanicus*
	Wet	- pupal mortality low - development very slow	- as for *P. pensylvanicus* - development slow, but faster than for *P. pensylvanicus*

6.2.3. Discussion

I believe there are two main principles behind the *P. adstrictus* population decrease, and the apparent constancy of the population of *P. pensylvanicus*.

1. These changes are thought to be related to differences in oviposition behaviour and sites, to the egg sensitivity to desiccation, and to moisture conditions (moisture concentration and evaporation rate). Thus, in the spring of 1967 the moisture conditions in the soil as well as in the logs were excellent, but later in the summer and in the fall, the moisture level dropped, especially in the logs, although moisture below the soil was still adequate. Thus, in 1968, the population size of each species remained almost the same. In the spring of 1968, until mid-June, the moisture level decreased even more, so most of the logs were dried up by June (estimated by touch only), while under the litter the moisture was still adequate (estimated by touch). In this period, eggs in the log habitat were probably killed, while in the soil the conditions remained viable for the eggs. Thus, fewer adults were produced in the fall of 1968, and in the spring of 1969 the trapping rate of *P. adstrictus* was lower. Because the moisture conditions in the spring of 1969 and 1970 were good in the logs, egg mortality due to drying of the habitat was probably low so changes in these years may have been due to other factors.
2. These changes probably are related to average temperature in the chosen habitat, as it affects the development rate. Thus, the size of the future population depends on the proportion of immatures reaching the adult stage before winter. *P. adstrictus* pupae usually completed their eclosion in September, but in 1970, probably because of the

wetter summer and consequent cooler conditions, the emergence was not complete as the peak occurred only three weeks before winter arrived. *P. pensylvanicus* pupae eclosed later than those of *P. adstrictus* on average. In 1968, 1969 and 1970, their emergence was incomplete as adults emerged until winter.

In conclusion, population size for both species at George Lake is probably controlled mostly by weather components. The most important ones are thought to be moisture and average temperature.

6.3. Attempt to Explain Differences in the Present Distribution of Each Species

As already discussed, *P. adstrictus* is spread across the boreal forest northward to the tundra, while *P. pensylvanicus* is found across the southern boreal forest and in the mixed forest, although it does not reach the west coast.

The data available permit a discussion of only the northern limit of both distributions, and of the western limit of *P. pensylvanicus* distribution.

The development rate is the primary subject of this discussion. Both species require the same time to develop from egg to adult under similar conditions (as tested at 20 C). Between the northern limit of distribution of each species, one main difference exists: the duration of the warm season. Thus *P. adstrictus*, whose distribution extends farther north, must be able to complete its development faster in order to survive with the shorter summer.

P. pensylvanicus populations reach their northern limit about 300 miles north of Edmonton at Fort MacMurray (Lindroth, 1966). Even near Edmonton, the percentage of pupae emerging is partially curtailed by the arrival of winter.

I assumed that average temperature of the chosen environment was the key to faster development. So each species was under evolutionary pressure to choose an environment which would submit the immature stages to warmer temperatures. The solution was different for each of the species. *P. adstrictus* females chose to oviposit in logs or in open habitats, while *P. pensylvanicus* females restricted their oviposition habitat from a wide range of forest litters in southern Canada to the litter of open well-drained deciduous forests at George Lake. Apparently, from George Lake data, the logs offer warmer average temperatures than under the litter or in the soil below the litter. Thus, the female and larval behaviour of *P. adstrictus* explains why the immatures of that species complete their development earlier than those of *P. pensylvanicus*, and also why the range of *P. adstrictus* can extend farther north.

P. pensylvanicus populations extend only as far west as central British Columbia. Specimens of *P. pensylvanicus* may have passed north of the prairies to British Columbia since the last glaciation as they are restricted to forest litter. On the other hand, this far north, *P. pensylvanicus* can develop only in the litter of open aspen forests. Thus, most of the Rockies present a wide and dark coniferous barrier except in the Peace River area where the widespread aspen forest still crosses the Rockies into central British Columbia. Further west, *P. pensylvanicus* is stopped by another coniferous barrier on the coastal range.

6.4. Discussion of Isolating Mechanisms Involved in the Recognition of the Species and of the Females by the Males of Each Species

Reproductive isolation of these two forms is indicated by concordant

distribution of several character states with no individuals showing intermediate combinations of these states. What are the isolating mechanisms, and are they pre- or post-mating in time of operation?

In the experiments discussed previously, males did not attempt to mate with females of a different species. Thus, the isolating mechanism probably operates in the precopulatory phase. The primary precopulatory mechanisms involved could be sense of touch, smell, taste, hearing and vision.

Some of these senses are probably not involved. One experiment suggested that males are not attracted by the sense of 'smell' through a volatile pheromone. There is no evidence for sound transmitting and receiving organs in these species, so 'hearing' is probably not involved. Copulation occurs in the dark, so 'vision' is probably not involved. Therefore, the only senses which may operate as isolating mechanisms are those of 'touch' and 'taste'.

Data on the behaviour of the precopulatory phase can give a clue about the isolating mechanisms involved. I made most of my basic observations on *Platypatrobus lacustris* Darl., *Nebria gyllenhali* Sch. and *Pterostichus punctatissimus* Rand.; but I present here only observations made on the two species concerned.

In the laboratory, beetles move apparently at random in the rearing boxes without much consideration for others as they do not especially avoid or seek other beetles. However, at short distances, perhaps when palps touch, there may be some interaction. Most of this interaction is of no consequence as the beetles just change their pathway. Sometimes a copulation may occur, but only if the female is approached by the male from behind (observed more than 100 times with the above named species). However, this approach does not always result in mating. There is probably some kind of

triggering mechanism so the male knows if the female belongs to his species, and if she is receptive. There is little doubt about the existence of a signal mechanism operating as mating occurs in specific periods. Even during the mating season, few females are receptive in *P. pensylvanicus* and *P. adstrictus* and those only for a short period. I suspect that they mate only once as I have not observed a mated female mating again.

If sense of 'touch' were involved, there should be some morphological difference in the surface near the apex of the female abdomen, but none is yet evident. Because of the rapidity of the transmitted information and its temporary transmission, I suspect that the isolating mechanism is a message of chemical origin that can be sensed by the palps.

More research is needed to solve the problem of the isolating mechanisms, and the area suggested by my studies is the non-volatile pheromones probably emitted by the apical region of the female abdomen.

6.5. Adaptive Significance of Behavioural and Morphological Characteristics Studied

6.5.1. Introduction

Each of the characteristics studied was probably developed, and is maintained, through the interaction of environment and gene pool, i.e. through natural selection. The result of natural selection is adaptation. In this section I attempt to indicate the adaptive value of the studied characteristics under present conditions. In the following section, I consider the possible historical antecedents of these characteristics in relation to the phylogeny of *P. adstrictus* and *P. pensylvanicus* and their close relatives.

6.5.2. Characteristics and Their Positive Selective Values Under Present Conditions

Habitats of Adults and Immature Stages

In general, adults and larvae live in the same general habitat although the larval habitats are usually more restricted.

Because oviposition is linked to the spring activity period of the adults, it is an important adaptation that the adults remain in the general habitat that is suited to the immature stages in order to prevent oviposition in unfavourable habitats. In the fall activity period, there is no oviposition, and the adults may occupy a much wider range of habitats. The adults spend the quiescent period and the winter diapause in similar habitats to those occupied in the spring, and the soils of these habitats are not subject to soaking. This is an important adaptation, as it encourages a higher adult survival rate by decreasing mortality due to drowning, and to freezing in ice.

Why are the immature stages of *P. adstrictus* restricted to logs, and those of *P. pensylvanicus* to the soil below the leaf litter? My studies of some of the environmental requirements indicate the answer may be, at least partially, that development rate is dependent on environmental temperature. The logs and well-drained forest litter probably provide warmer average conditions than the average conditions found in the other forest litter habitats (as found at George Lake). Thus these habitats provide an overall higher development rate for immature stages. But the logs also tend to be more variable in this respect than is the forest soil, and hence there may be a higher mortality of *P. adstrictus* eggs than of *P. pensylvanicus* eggs. Therefore the microhabitats chosen by the females for oviposition involve a conflict between higher development rate and higher survival rate, and this

conflict has been solved differently by the two species.

Reproduction

The behaviour of the females in choosing the necessary environmental conditions for oviposition is an important adaptation for insuring the success of the species from year to year. From the available evidence, I believe that the egg stage is critical as it depends on stable conditions of moisture for survival. In this respect, *P. pensylvanicus* is better adapted because the females usually choose very moist conditions. *P. adstrictus* females counteract the higher egg mortality rate by laying more eggs earlier.

Females lay eggs in batches. The simultaneous existence of features of the preferred habitat, including soil structure, texture, and moisture, may serve as a triggering mechanism for oviposition. The 'preferred' sites are rare, so when such a site is found it is important that the female has adapted to lay numerous eggs. If only a few eggs were laid each time such a habitat were encountered, the number of offspring would be much reduced, and the survival of the population endangered. Thus females accumulate their eggs until suitable habitats are encountered.

Thiele (1968b) pointed out that most carabids reproduce in summer. This suggests that spring reproduction is not characteristic of forest litter species, although a spring cycle may help in reducing competition among forest litter carabids by separating the spring carabids from the summer carabids.

Adults of both species are most active in spring. Most of this activity is linked, apparently, with the search for food, as I found most of the full crops in both sexes in spring. The search for food is important for providing energy for egg production, and for searching for suitable oviposition sites.

Hence, the spring activity cycle is linked with the success of oviposition.

After the spring activity, adults enter a summer quiescent period. The quiescent period experienced by adults of the species helps reduce competition with other carabids, especially their own larvae, and so may be of adaptive significance.

There is another lesser activity peak in the fall, due primarily to emergence of new adults which search for food, mates and winter quarters. The adults which spend the summer in aestivation enter the winter diapause with or without fall activity. So the fall activity peak is probably important for the development of fat reserves in the new adults, and for increasing the number of fertilized females, and consequently is significant in the survival of the species.

Mating

Mating adaptations are similar in both species. Apparently, most of the mating behaviourisms are linked to the absence of attractants, so the females and males probably encounter each other at random. In both species there are as many males as females, females are receptive in the fall (at least in *P. pensylvanicus*), and again in spring until early June, and females have spermathecae (preserving sperm for at least three months, and probably nine). All these characteristics help to insure that there is a high proportion of mated females.

6.5.3. Conclusions

These two species are morphologically and behaviourally similar. Because of their sensitivity to desiccation, I believe that the eggs play a critical role in the success of the population (especially in *P. adstrictus*). Females oviposit in batches, thus insuring that eggs will be in a suitable

habitat, and that high numbers are laid. Females of both species oviposit only in spring, so new adults appear before the winter (apparently only adults of these species can diapause). Spring reproduction is linked with the spring peak of activity. Both species have long mating periods, males are as abundant as females, and females have spermathecae.

The species also differ in some characteristics. The habitats of the species are similar where their distributions overlap, but *P. adstrictus* is much more eurytopic (Lindroth, 1966; Frank, 1971), and occurs in numerous habitats where *P. pensylvanicus* does not. Immatures of *P. adstrictus* inhabit logs, those of *P. pensylvanicus* inhabit the soil under the leaf litter. These different habitats are advantageous with respect to the higher development rate, but result in a higher mortality rate for *P. adstrictus* eggs. The disadvantages are counterbalanced in *P. adstrictus* populations by a higher oviposition rate, an earlier oviposition period, and faster egg development than *P. pensylvanicus* populations.

6.6. Relationship Between *P. adstrictus* and *P. pensylvanicus* and Their Past History

6.6.1. Introduction

After studies of other related species (i.e. members of the subgenera *Bothriopterus* and *Dysidius*), I feel that *P. adstrictus* and *P. pensylvanicus* are not as closely related as first anticipated, in spite of their many ecological, morphological and behavioural similarities. Further study of the morphological characters and the possible relationships of these two species, as well as those of all Nearctic *Bothriopterus* and *Dysidius* was made. In this section, I attempt to show the relationships between *P. adstrictus* and *P. pensylvanicus* with reference to known American species of *Bothriopterus*

and *Dysidius;* to explain the past history of each species with reference to known relationships and distributions; and, on the basis of the preceding postulations I attempt to outline the history of the behavioural characteristics with special reference to *P. adstrictus* and *P. pensylvanicus*.

6.6.2. Phylogenetic Relationships Derived from Morphological Characteristics of Adults

In the Nearctic Region, five species are related to *P. adstrictus* and *P. pensylvanicus*. This association has been pointed out by Lindroth (1966) with special reference to the type of median lobe in the male (shape and absence of internal sclerites). This group of seven species is part of two subgenera: *Bothriopterus* (four species including *P. adstrictus* and *P. pensylvanicus*), and *Dysidius* (three species). *Dysidius* was defined by the presence of three unexpanded foveae on the disc of each elytron, and similar male and female microsculpture. These differences are weak as *P. pensylvanicus* specimens have poorly expanded elytral discal foveae and nearly similar male and female microsculpture, and as *P. tropicalis* and the European *P. angustatus* specimens have only three discal foveae. To determine relationships, an analysis of characteristics of Nearctic species was made (Table 10). I have attempted to explain the evolution of characters in the simplest way, as I assumed that a character cannot be regained after being lost (Dollo's Law). If a diagram of relationships did not comply entirely with this principle, I discarded it. The most difficult task was to determine if a character was plesiotypic or apotypic. To comply with Dollo's Law, three discal foveae and unexpanded umbilical foveae were considered primitive among the species studied. The sharp apex of the median lobe in dorsal view, the small size of the spermatheca, and the presence of a brush on the hind tibia, were considered as apotypic for single species in well-defined

Table 10. Code number and classification of structural characters studied.

Character	Character designation	Evolutionary state of the character	
		Plesiotypic	Apotypic
Pronotal basal bead	1	incomplete	complete
Number of elytral discal foveae	2	three	five
Diameter of elytral discal foveae	3	expanded	not expanded
Diameter of foveae of the umbilicate series	4	not expanded	expanded
Brush on interior hind tibia of males	5	absent	present
Apex of median lobe in dorsal view	6	wide	narrow
Shape of spermatheca	7	globular	elongate
Size of spermatheca	8	large	small

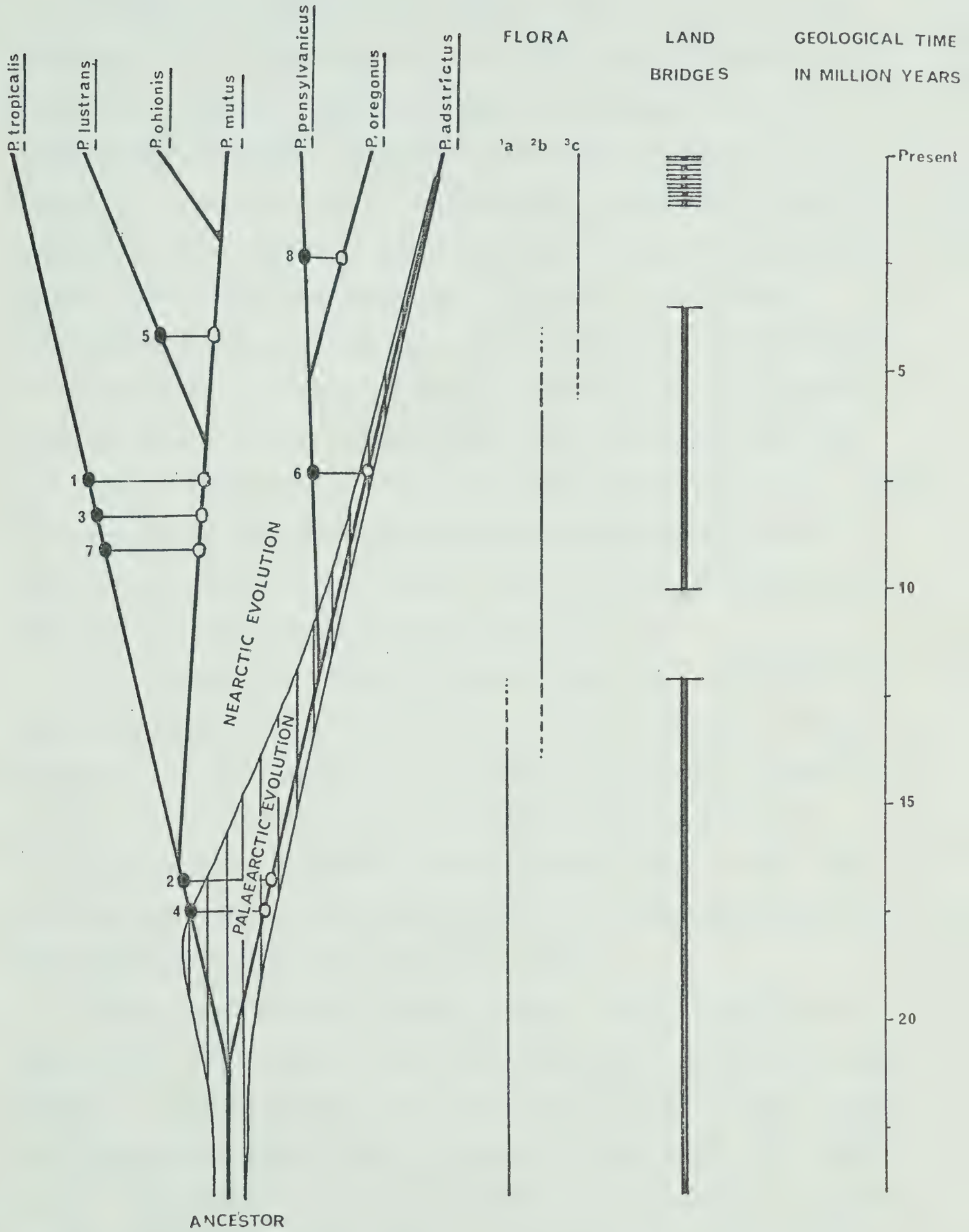
subgroups. The incomplete pronotal bead and the expanded dorsal discal foveae were considered plesiotypic to comply with Dollo's Law. Thus, with the analysis of the data, a phylogeny showing the relationships among the species was illustrated (Fig. 12) where the most primitive form is *P. tropicalis*, and the most derived one is *P. adstrictus*. Because I see no important reason for separating *P. tropicalis* from *Bothriopterus*, and as the *Dysidius* are considered derived from the *P. tropicalis* ancestor, I have considered all the species studied here as members of a single subgenus, *Bothriopterus*.

6.6.3. Past History of Nearctic *Bothriopterus*

From the evidence of present distributions, the past evidence of land bridges, the past changes in flora, and probable relations among the Nearctic *Bothriopterus*, the following past history may be postulated. First, *Bothriopterus* today forms two main groups: a boreal one with *P. adstrictus*, and a temperate one with the remaining species. Second, only *P. adstrictus*, which is still very widespread in Eurasia, may be considered to be closely related to Eurasian species. Third, the most diversified branches of *Bothriopterus* are found in Eurasia (Tschitscherine, 1900; Lindroth, 1945; Jedlička, 1962). These three points suggest that the area of origin of the Nearctic *Bothriopterus* is Eurasia, and that there were at least two widely separated periods of introduction of the Nearctic *Bothriopterus* into the Nearctic Region, one rather recent, and one or two very old.

Eurasia and the Nearctic Region were united in three main periods: in the Miocene until 12 million years ago, in the late Miocene from 10 million to 3.5 million years ago, and repeatedly in the Pleistocene with the advance and retreat of the ice sheet (MacGinite, 1958; Hopkins, 1967; Repenning, 1967).

Fig. 12. Diagram of the phylogeny of the Nearctic species of *Bothriopterus* in relation to geological time, land bridges in the Beringia area, forest cover in Beringia, and time of arrival in the New World.



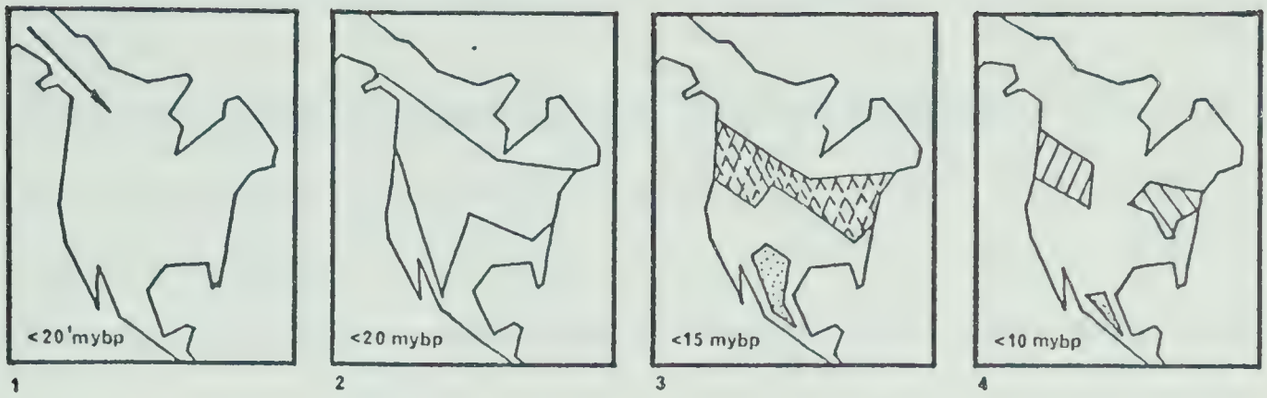
[1]arcto-tertiary forest
[2]coniferous forest
[3]taiga

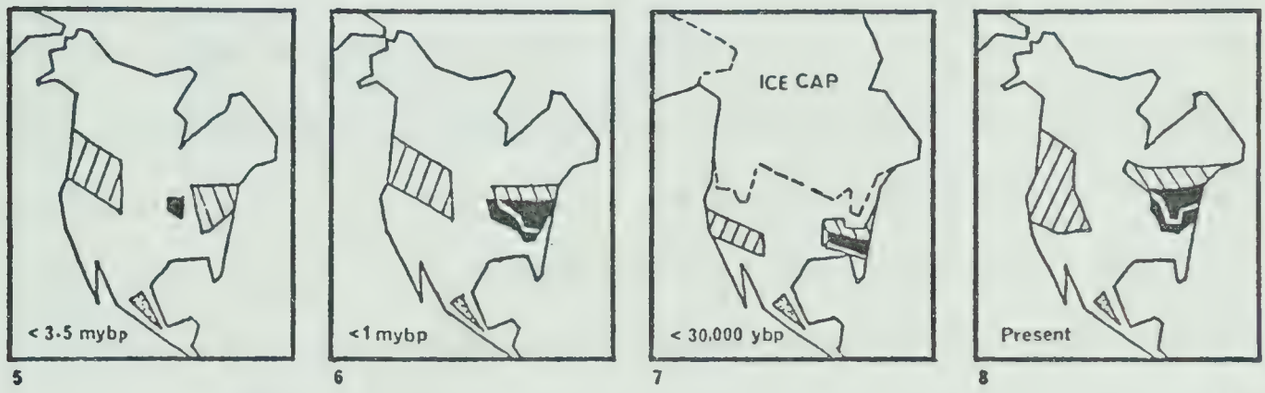
Because *P. adstrictus* did not speciate in the Nearctic Region, I believe that it arrived during the Pleistocene (probably invading more than once, as Lindroth [1966] shows evidence of subspeciation in the Aleutians and California). Because the other Nearctic species are very different from Eurasian species, I believe they evolved here a long time ago, and may have invaded the Nearctic Region at one of the two periods of land connections during the Miocene. Because *P. oregonus* and *P. pensylvanicus* are adapted to more northerly climates (though mostly south of the boreal forest), I believe that the ancestor of these two species came less than 10 million years ago when a mixed and boreal forest was developing over the Beringia (Wolfe and Leopold, 1967; Hopkins et al., 1971). Also, because the remaining species are restricted to warmer climates (usually the deciduous forest biome), I believe that their ancestor came more than 12 million years ago (summarized in Fig. 13).

How did speciation produce the present fauna? What could have interrupted gene flow to produce effective reproductive isolation? Probably (especially for species with similar general requirements), prolonged geographic isolation provided by natural barriers occurring during the geological periods provided the necessary isolation (Mayr, 1969). The barriers of greatest interest here are shifts in average temperature, and development of the ice sheets and of the prairie.

I believe that the first Nearctic invader, the *P. tropicalis* and *P. mutus* group ancestor, spread widely over North America and northern Central America. Later the originally continuous range was separated into northern and southern populations by the development of grasslands in the southern U.S.A. The southern population became what we know today as *P. tropicalis* which is restricted to high altitudes in southern Mexico. The northern

Fig. 13. Diagrammatic sequence of *Bothriopterus* evolution in the New World. Diagrams 1 to 8 represent the first invasion giving *P. tropicalis*, *P. lustrans*, *P. mutus*, and *P. ohionis*. Diagrams 9 to 13 represent the second invasion giving *P. oregonus* and *P. pensylvanicus*. Diagrams 14 to 17 represent the third invasion by *P. adstrictus*.



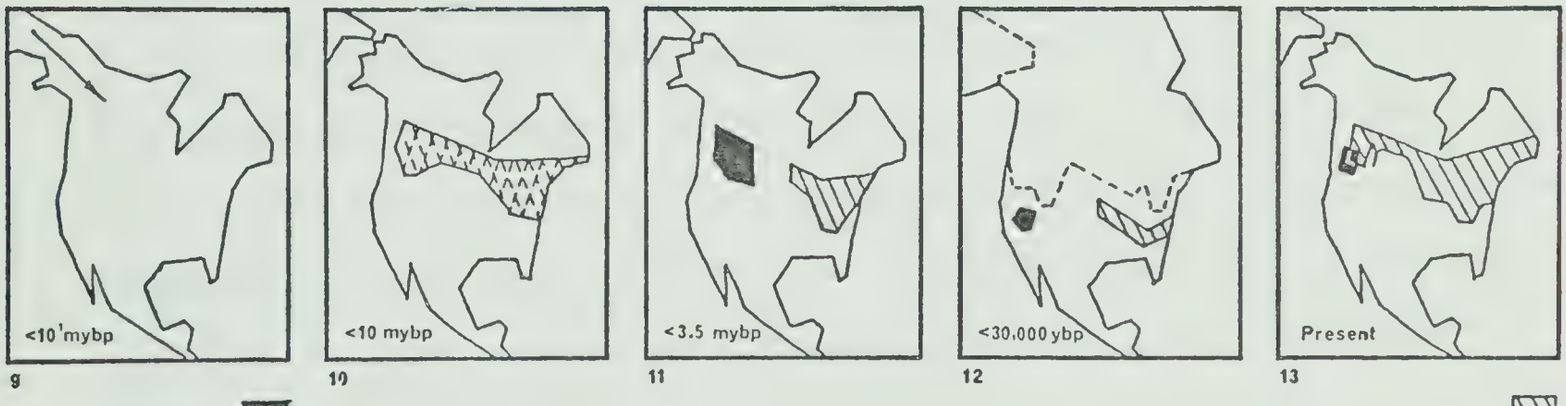


P. tropicalis

P. lustrans

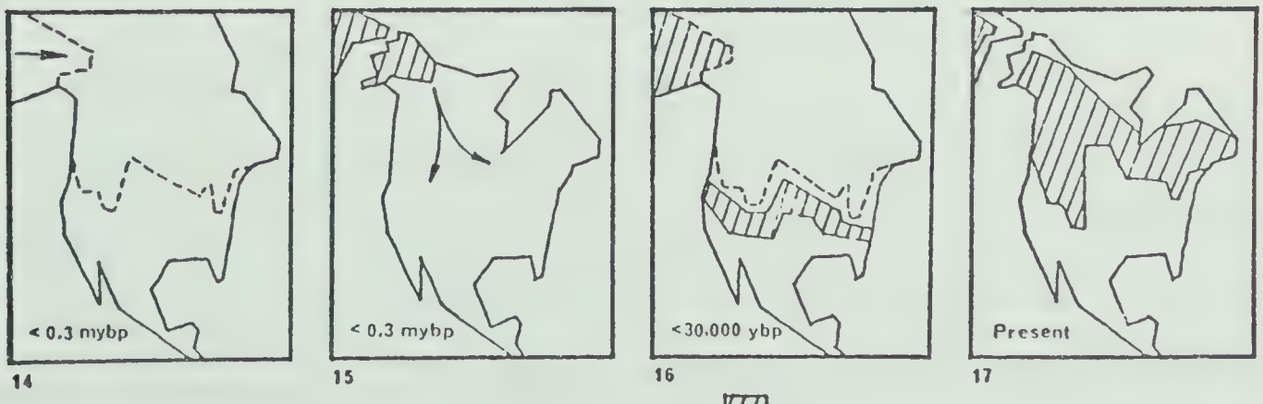
P. mutus

P. ohionis



P. oregonus

P. pensylvanicus



P. adstrictus

population was separated into eastern and western populations with the northward development of the southern grassland. In time the western population became *P. lustrans*, and the eastern one became *P. mutus* and *P. ohionis* (a more southern species than *P. mutus*). These last three species are thought to have evolved in the Nearctic Region as no close relative seems to be known in Asia (Jedlička, 1962).

The second invader of North America spread in more northerly regions of North America than the ancestor of the *P. mutus* group, as it was more cool-adapted. Because the southern grassland moved northward, and the cooler climate extended further south, the ancestral population was divided into western and eastern populations. The western population became *P. oregonus* and the eastern one, *P. pensylvanicus*.

As the climate cooled in the Pliocene and early Pleistocene, and land bridges repeatedly were formed in the Pleistocene with the development of the continental ice cap, *P. adstrictus* invaded Alaska which was then unglaciated. In the subsequent warming of the climate, *P. adstrictus* passed south of the ice sheet (Coope, 1968a and 1968b). With successive extension and withdrawal of the ice sheet further invasion by this boreal species probably occurred. Today the Alaskan and continental populations are found together again.

6.6.4. Past History of the Behavioural Characteristics Studied in *P. adstrictus* and *P. pensylvanicus*

The many ecological character states shared by *P. pensylvanicus* and *P. adstrictus* lead to a question about each similarity: is it plesiotypic or apotypic? If apotypic, the similarity must be the result of convergent evolution because the two taxa are not sister species. In the case of differing character states, one may ask which of the two is plesiotypic,

which is apotypic, or are both apotypic? To answer the question, data must be available on the distribution of the character states among the other species of *Bothriopterus*. At present, such data are available for geographical distribution, habitat, and overwintering. The history of these characteristics only is considered further.

From the present distributions, three main groups may be seen: a boreal group, a temperate group, and a sub-tropical group. As the subgenus probably originated in Eurasia, a species with a southern distribution is thought to be older than a northern one. As the climatic conditions cooled in time, first the warm-adapted, then the cool-adapted, and finally the cold-adapted species arrived. There was probably little or no displacement of already existing species as the invaders established themselves in the climatic zone for which they were already adapted. Thus, a northern distribution is considered apotypic with respect to a southern one. So, the distribution of *P. pensylvanicus* is considered plesiotypic relative to that of *P. adstrictus*.

From the knowledge of the habitats of the extant species (Lindroth, 1966; Ball, personal communication) the three ancestors must have been unable to withstand very dry conditions, and probably lived in open habitats quite independent of litter habitats. Thus, the litter specialization in *P. pensylvanicus* is considered apotypic, while the adaptation of *P. adstrictus* to both litter and open habitats is considered plesiotypic.

As far as is known, all adults of *Bothriopterus* in temperate regions winter only as adults (one exception of *P. adstrictus* reported by Lindroth [1955] and probably the Belleville *P. pensylvanicus* population reported by Rivard [1964]). Thus adult overwintering probably evolved from the ancestral habit of living in open habitats. Thus, adult overwintering in *P. adstrictus*

and in the Alberta population of *P. pensylvanicus* is considered plesiotypic.

6.6.5. Local Adaptation Problems

Many interesting local special features have been observed in *P. pensylvanicus*. Such special features point out many problems that need further investigation. In eastern Canada (around Montreal) this species is found in various forest litter habitats including coniferous litter; in central Canada (Thunder Bay, Ontario), Freitag (personal communication) found that *P. pensylvanicus* is apparently restricted to coniferous litter habitats; and, at George Lake it is restricted entirely to deciduous litter habitats. In Belleville, Ontario, Rivard (1964) discovered that females of *P. pensylvanicus* oviposit only in mid- and late summer, while in Montreal I suspect a spring oviposition because I have collected teneral adults only in late summer. These local observations bring a few questions. Is *P. pensylvanicus* one or more species? If it is one species, does it form isolated populations? If not, what are the patterns of the local evolutionary trends? What are the evolutionary pressures?

Such questions open the door for further comparative research over the total range of each species as these studies can illustrate principles behind speciation.

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